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STUDIES IN THE GENUS *CERATIUM* SCHRANK WITH REFERENCE TO SPECIMENS COLLECTED IN THE AGULHAS CURRENT: 3.

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ABSTRACT

A taxonomic account is given of Subsection *Macroceras* Ostf., incorporating the use of polar co-ordinate measurements of antapical horn curvature in descriptions and delimitation of species.

UITTREKSEL

STUDIES IN DIE GENUS *CERATIUM* SCHRANK MET VERWYSING NA MONSTERS IN DIE AGULHASSTROOM VERSAMEL: 3.
'n Taksonomiese verslag van die subseksie *Macroceras* Ostf. wat polêre koordinate van antapikale horing geboëndheid in die beskrywing en afbakening van die soorte gebruik.

INTRODUCTION

The use of polar co-ordinates in measurement of antapical horn curvature in Section *Macroceras* Ostenfeld has already been discussed, (Reinecke 1973). For convenience the terminology used in the key and descriptions is again given.

TERMINOLOGY

Polar co-ordinates—degree and radius co-ordinates used here as a means of measuring the curvature of the antapical horns, plotted on camera lucida drawings of full dorsal or ventral aspect, at intervals of 15 μ, along the edges of the horns initially adjacent to the base of the hypotheca.

Radius unit—on the scale of the camera lucida drawings and the polar co-ordinate graph paper used, one radius unit is approximately equal to 3 μ. The radius units are sometimes given as R.U.

Zero point for radius co-ordinates—the point of inception of the antapical horn immediately adjacent to the base of the hypotheca.

Posterior line—a line drawn to pass through the zero points of the antapical horns.

Zero line for degree co-ordinates—determined by drawing lines through the zero points of the right and left horns perpendicular to the posterior line.

MRC—the maximum rate of change of direction of curvature of a horn

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measured in degrees over 15 μ after the initial curvature from 0–15 μ. (Very rarely, the MRC occurs over two, in exceptional cases three, successive 15 μ intervals.)

MBC—the point of maximum backward curvature of the horns, determined by the construction of a tangent to the posterior or lower edge of the antapical horn parallel to the posterior line.

$\frac{B}{H}$—ratio in which *H* is the perpendicular distance between a line joining the profile edges of the lower girdle list and a line parallel to it through the zero point for the radius co-ordinates of the left horn, and *B* is the perpendicular distance between this latter line and a line parallel to it drawn as a tangent to the lower edge of the left antapical horn.

$\frac{L90}{D}$ and $\frac{R90}{D}$—ratios in which *L90* and *R90* are the left and right horn radius co-ordinates with the 90° co-ordinate, and *D* is the girdle diameter measured in radius units.

$\frac{RMBC}{D}$—ratio in which *RMBC* is the right horn MBC radius co-ordinate in R.U.

In order to compare specimens illustrated in the literature with those seen in the Agulhas current NGY samples collected during International Geophysical Year 1958, it was necessary to make photographic enlargements at a scale similar to that of camera lucida drawings of the NGY specimens. In some cases the scale of the figures was unknown and it was impossible to estimate the girdle diameter, in other instances the scales could have been inaccurate and sometimes the drawings were poor.

Subgenus ORTHOCERATIUM Sournia (1967): 376.
Section MACROCERAS Ostenfeld (1903): 192.
Subsection MACROCERAS

DIAGNOSIS

Differs from Subsection *Robusta* Karsten in that chain formation is extremely rare, and the length of the apical horn in posterior members of a chain is greater than 0,4 times that of the anterior cell in a complete chain. Differs from Subsection *Reflexa* (Jörg.) Reinecke in that both antapical horns are anteriorly directed after the initial backward curvature.

KEY, USING POLAR CO-ORDINATE MEASUREMENTS OF ANTAPICAL HORN CURVATURE IN CAMERA LUCIDA DRAWINGS, TO TAXA OF SUBSECTION *MACROCERAS*.

(Based on specimens seen in Agulhas current NGY samples, sample IGY 121, from Oslo Fiord and on figures from the literature.)

I. Both antapical horns very obviously deflected ventrally
  (1) Right horn MBC radius co-ordinate $\geq 60\ \mu$ ... *C. deflexum f. sinensis*

(2) Right horn MBC radius co-ordinate $< 55\ \mu$
(i) Sum of left and right horn MRC's $> 50°$ *C. defluxum f. deflexum*
(ii) Sum of left and right horn MRC's $< 50°$ *C. deflexum f. deflectomassum*
II. Ventral deflexion of antapical horns slight or not possible to determine
A. Left horn MRC occurs beyond the 75 μ radius co-ordinate
(1) Left horn degree co-ordinate with 15 μ radius co-ordinate ≥ 90
(i) Girdle diameter $\geq 60\ \mu$ *C. massiliense var. massiliense**
(ii) Girdle diameter $\leq 57\ \mu$ *C. tenue**
(2) Left horn degree co-ordinate with 15 μ radius co-ordinate < 90
(i) Left horn MBC degree co-ordinate $\geq 70°$
(a) Right horn MBC degree co-ordinate $\leq 40°$ *C. deflexum f. sinensis*
(aa) Right horn MBC degree co-ordinate $> 40°$
(b) Girdle diameter $< 45\ \mu$ *C. trichoceros var. trichoceros*
(bb) Girdle diameter $> 48\ \mu$ *C. trichoceros var. contrarium*
(bbb) Girdle diameter 45–48 μ
(c) "Kink" present at base of left horn and/or ratio $\frac{\text{RMBC}}{\text{D}} > 1{,}75$ *C. trichoceros var. trichoceros*
(cc) "Kink" absent from base of left horn and ratio $\frac{\text{RMBC}}{\text{D}} < 1{,}75$ *C. trichoceros var. contrarium*
(ii) Left horn MBC degree co-ordinate $< 70°$
(a) Left horn MBC degree co-ordinate ≥ 65
(b) Right horn MBC degree co-ordinate $> 40°$
(c) Girdle diameter $> 45\ \mu$
(d) Right horn MRC $> 10°$ *C. macroceros*
(dd) Right horn MRC $< 10°$
(e) *Sum of left and right horn MRC's* $> 25°$ *C. macroceros*
(ee) Sum of left and right horn MRC's $< 25°$ *C. massiliense var. carriense**
(cc) Girdle diameter $\leq 45\ \mu$
α. Girdle diameter $< 45\ \mu$ *C. trichoceros var. trichoceros*
αα. Girdle diameter $= 45\ \mu$
β. "Kink" present at base of left horn and/or ratio $\frac{\text{RMBC}}{\text{D}} \wedge 1{,}75$ *C. trichoceros var. trichoceros*
ββ. *"Kink" absent from base of left horn and ratio* $\frac{\text{RMBC}}{\text{D}} < 1{,}75$ *C. trichoceros var. contrarium*
(bb) Right horn MBC degree co-ordinate ≤ 40
α. Difference between left and right horn MBC degree co-ordinates $\leq 20°$ *C. macroceros*
αα. Difference between left and right horn MBC degree co-ordinates $\geq 20°$
β. Sum of left and right horn MRC's $> 40°$, antapical horns smooth or with very minute denticles *C. deflexum f. sinensis*
ββ. Sum of left and right horn MRC's $< 40°$, antapical horns often very spiny *C. macroceros*
(aa) Left horn MBC degree co-ordinate $< 65°$
α. Ratio $\frac{\text{L90}}{\text{D}} \geq 2{,}00$ *C. macroceros*
αα Ratio $\frac{\text{L90}}{\text{D}} < 2{,}00$
β. Difference between left and right horn MBC degree co-ordinates $\leq 20°$ *C. macroceros*
ββ. Difference between left and right horn MBC degree co-ordinates $> 20°$ *C. deflexum f. sinensis*
AA. Left horn MRC occurs before the 75 μ radius co-ordinate
B. Ratio $\frac{\text{B}}{\text{H}} < 0{,}90$
C. Ratio $\frac{\text{B}}{\text{H}} \geq 0{,}80$

(1) Sum of left and right horn MRC's $\geq 40°$
(i) Sum of left and right horn MRC's $> 50°$
(a) Left horn degree co-ordinate with 105 μ radius co-ordinate $\geq 150°$ *C. deflexum f. deflexum*
(aa) Left horn degree co-ordinate with 105 μ radius co-ordinate $< 150°$
(b) Right horn degree co-ordinate with 105 μ radius co-ordinate $< 115°$ and difference between left and right horn MBC degree co-ordinates $\leq 20°$ *C. macroceros**
(bb) Right horn degree co-ordinate with 105 μ radius co-ordinate $> 115°$ and/or difference between left and right horn MBC degree co-ordinates $> 20°$ *C. deflexum f. deflexum*
(ii) Sum of left and right horn MRC's $\leq 50°$ *C. deflexum f. deflectomassum*
(2) Sum of left and right horn MRC's $< 40°$
(i) Left horn degree co-ordinate with 150 μ radius co-ordinate $> 130°$ *C. massiliense var. massiliense*
(ii) Left horn degree co-ordinate with 150 μ radius co-ordinate $< 130°$ *C. massiliense var. carriense*

CC. Ratio $\frac{B}{H} < 0{,}80$
(1) Right horn degree co-ordinate with 15 μ radius co-ordinate $\geq 45°$
(i) Girdle diameter $\leq 57\ \mu$ *C. tenue*
(ii) Girdle diameter $\geq 60\ \mu$
(a) Left horn degree co-ordinate with 150 μ radius co-ordinate $> 130°$ *C. massiliense var. massiliense*
(aa) Left horn degree co-ordinate with 150 μ radius co-ordinate $< 130°$ *C. massiliense var. carriense*
(2) Right horn degree co-ordinate with 15 μ radius co-ordinate $< 45°$
(i) Sum of left and right horn MRC's $\geq 40°$
(a) Left horn degree co-ordinate with 150 μ radius co-ordinate $< 130°$ *C. massiliense var. carriense**
(aa) Left horn degree co-ordinate with 150 μ radius co-ordinate $> 135°$
(b) Sum of left and right horn MRC's $> 50°$ *C. deflexum f. deflexum*
(bb) Sum of left and right horn MRC's $\leq 50°$ *C. deflexum f. deflectomassum*
(ii) Sum of left and right horn MRC's $< 40°$
(a) Left horn degree co-ordinate with 150 μ radius co-ordinate $> 130°$ *C. massiliense var. massiliense*
(aa) Left horn degree co-ordinate with 150 μ radius co-ordinate $< 130°$ *C. massiliense var. carriense*

BB. Ratio $\frac{B}{H} \geq 0{,}90$
(1) Ratio $\frac{B}{H}$ — $< 1{,}10$
(i) Right horn MRC $\leq 10°$
(a) Girdle diameter $\geq 60\ \mu$
(b) Sum of left and right horn MRC's $> 25°$ *C. macroceros**
(bb) Sum of left and right horn MRC's $< 25°$ *C. massiliense var. carriense*
(aa) Girdle diameter $< 57\ \mu$ *C. macroceros**
(ii) Right horn MRC $> 10°$
(a) Left horn degree co-ordinate with 105 μ radius co-ordinate $\geq 150°$
(b) *Right horn MBC radius co-ordinate* $\geq 60\ \mu$ *C. deflexum f. sinensis*
(bb) Right horn MBC radius co-ordinate $< 55\ \mu$
(c) Sum of left and right horn MRC's $> 50°$ *C. deflexum f. deflexum*
(cc) *Sum of left and right horn MRC's* $\leq 50°$ *C. deflexum f. deflectomassum*
(aa) Left horn degree co-ordinate with 105 μ radius co-ordinate $< 150°$

α. Difference between left and right horn MBC degree co-ordinates $\leq 20°$
  β. Right horn degree co-ordinate with 105 μ radius co-ordinate $> 115°$ *C. deflexum f. deflexum*
  ββ. Right horn degree co-ordinate with 105 μ radius co-ordinate $< 115°$ *C. macroceros*
αα. Difference between left and right horn MBC degree co-ordinates $> 20°$
  (/) Left horn degree co-ordinate with 105 μ radius co-ordinate $> 135°$
    (+) Right horn MBC radius co-ordinate ≥ 60 μ *C. deflexum f. sinensis**
    (++) Right horn MBC radius co-ordinate < 55 μ
      (*) Sum of left and right horn MRC's > 50 *C. deflexum f. deflexum*
      (**) Sum of left and right horn MRC's $\leq 50°$ *C. deflexum f. deflectomassum**
  (//) Left horn degree co-ordinate with 105 μ radius co-ordinate $< 135°$ *C. macroceros*

(2) Ratio $\frac{B}{H}$ — $\geq 1{,}10$ but $< 1{,}50$
  (i) Difference between left horn radius co-ordinates of tangent parallel to girdle and of point of MBC > 100 μ *C. massiliense var. carriense*
  (ii) Difference between left horn radius co-ordinates of tangent parallel to girdle and of point of MBC < 100 μ
    (a) Right horn MRC $< 10°$ and sum of left and right horn MRC's < 25 *C. massiliense var. carriense*
    (aa) Right horn MRC $> 10°$, sum of left and right horn MRC's rarely $<$ 25°, never $< 20°$
      (b) Left horn degree co-ordinate with 105 μ radius co-ordinate ≥ 150
        (c) Difference between left and right horn MBC degree co-ordinates $< 10°$ *C. macroceros**
        (cc) Difference between left and right horn MBC degree co-ordinates $> 15°$ *C. deflexum f. deflexum**
      (bb) Left horn degree co-ordinate with 105 μ radius co-ordinate < 150 *C. macroceros*

(3) Ratio $\frac{B}{H} \geq 1{,}50$ *C. macroceros*

Ceratium macroceros (Ehrenberg) Vanhoeffen (1897): 310, 382, Pl. 5, Fig. 10. Okamura & Nishikawa (1904): 122, Pl. 6, Fig. 2; Paulsen (1908): 81, Fig. 109 (= Bergh (1882) Fig. 27); Jörgensen (1911): 63, Pl. 1, Fig. 6 (heteromorphic chain), Pl. 7, Figs. 132a, b, 133; Mangin (1912): 25, Fig. 10; Dangeard (1926): 315, Fig. 4c; Abé (1927): 427, Fig. 44A–E; Peters (1932): 47, Pl. 4, Fig. 17b; Wang (1936): 160, Fig. 29; Schiller (1937): 428, Fig. 468a, b (heteromorphic chain), ?c and ?d (solitary heteromorphs), (from Peters, reference not given); Silva (1949): 360, Pl. 7, Fig. 2, Pl. 9, Fig. 11; Margalef & Duran (1953): 42, Fig. 12a–e, ?f (solitary heteromorph); López (1966): 330, Fig. 16.

? e.p. Lebour (1925): 155, *non* Pl. 35, Fig. 1 (= *C. tenue* O. & S.); ? e.p. Wood (1954): 310, *non* Fig. 238a (either *C. massiliense var. massiliense* (Gour.) Kars. or *C. deflexum f. deflectomassum* Rein.); ? e.p. Klement (1964): 357, *non* Pl. 3, Fig. 1 (= *C. deflexum f. deflectomassum*).

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* Indicates a single specimen recorded with these dimensions. The portions of the key in italics are included for the sake of completion, as specimens with these dimensions were not measured.

Non Ostenfeld & Schmidt (1901): 167, Fig. 19 (= *C. deflexum f. deflexum* (Kof.) Jörg.); *non* Wailes (1928) Pl. 11, Figs. 16–18 (= *C. tenue* and *C. longipes* (Bail.) Gran); *non* Ballantine (1961): 225, Fig. 56 (Either *C. deflexum f. deflectomassum* or *C. massiliense var. massiliense*).

Mentioned without illustration as *C. macroceros* by: Pavillard (1905): 53; (1907): 225; (1931): 87; Schröder (1906); Forti (1922): 62; Dangeard (1927): 377; Gaarder (1954): 14; Silva (1956); (1960); Braarud, Foyne & Hasle (1958); Travers and Travers (1962): 58; Mulford (1963): 86; Wood (1963): 12; Taylor (1967): 463; Nel (1968); Thorrington Smith (1969); (1971); Hasle (1969): 152.

"*C. macroceros* Ehrb. f." Okamura (1907): 128, Pl. 4, Fig. 19.

"*C. macroceros* (Ehrb.) f.?" Abé (1927): 428, Fig. 46.

Non "*C. macroceros* Ehrb. f. ?" Okamura (1907): 128, Pl. 4, Fig. 20a, b (= *C. deflexum f. deflexum*).

C. macroceros subsp. macroceros: Graham & Bronikowsky (1944): 37, Fig. 21F.

C. macroceros var. macroceros: Sournia (1966): 1982; (1967): 460, Fig. 83 (= Jörgensen (1911) Fig. 133).

Peridinium macroceros Ehrenberg (1840): 201.

C. tripos Nitzsch var. *α Per. macroceros* (Ehr.) Claparède & Lachmann (1859): 397, Pl. 19, Fig. 1.

C. tripos var. macroceros: Gourret (1883): 26, Pl. 2, Fig. 41; Cleve (1897): 301, Pl. 1, Fig. 6; ? Schröder (1900): 15, Pl. 1, Fig. 17f (peculiar form with unusually long right horn MBC radius co-ordinate).

Listed without figure as *C. tripos var. macroceros* by: Zacharias (1906): 543.

C. tripos macroceros: Entz (1902): 100, e.p., Pl. 2, Fig. 15, ?13, ?14 (solitary heteromorphs), ?16 (only body and bases of horns shown), *non* 17 and 18 (= *C. massiliense var. massiliense*); Karsten (1906): 145, ep., Pl. 22, Fig. 29b–d, *non* a (= *C. massiliense var. massiliense*); (1907): 411, e.p., Pl. 49, Fig. 27b, *non* d (= *C. massiliense var. carriense* (Gour.) Rein.).

C. macroceros var. karstenii Abé (1927): 427, Fig. 45.

C. macroceros var. gallicum (Kofoid) Sournia (1966): 1982; (1967): 462, Fig. 84; Steidinger & Williams (1970): 46, Fig. 29a, b.

"*C. macroceros var. gallicum* (Kof.) Jörg." Schiller (1937): 430, Fig. 469 (= Jörgensen (1911) Fig. 134); Rampi (1939): 310, Fig. 42; Halim (1960): 180, Pl. 5, Fig. 7.

Mentioned without illustration as "*C. macroceros var. gallicum* (Kof.) Jörg." by: Gaarder (1954): 14; Klement (1964): 358.

Mentioned without illustration as "*C. macroceros var. gallicum*" by: Nel (1968).

"*C. macroceros f. gallicum* (Kof.) Jörg." Halim (1963): 498, Fig. 27.

C. macroceros subsp. gallicum (Kof.) Jörgensen (1911): 63, Pl. 7, Figs. 134, 135; (1920): 83, Fig. 77; Forti (1922): 64, Pl. 3, Fig. 48 (= Jörgensen (1911) Fig. 134); Abé (1927): 429, Fig. 47A–D; Paulsen (1930): 87, Fig. 54A–C; Böhm (1931b):

38, Fig. 35a; Steemann Nielsen (1934): 25, Fig. 59; Graham & Bronikowsky (1944): 37, Fig. 21B, D, E *non* C (= *C. deflexum f. deflectomassum*); Wood (1954): 311, Fig. 238b.

Mentioned without illustration as *C. macroceros subsp. gallicum* by: Schröder (1911): 646; Böhm (1931a): 364; Pavillard (1931): 88; Steemann Nielsen (1939): 14; Silva (1949): 360; (1956).

C. macroceros "*gallicum* > *macroceros*" Sournia (1967): 464, Fig. 85.

C. macroceros "*macroceros—gallicum*" Sournia (1966): 1982.

C. gallicum Kofoid (1907b): 302, Pl. 24, Figs. 10–12.

Mentioned without illustration as *C. gallicum* by: Wood (1963): 9.

C. tripos macroceras var. crassa Karsten (1907): 411, e.p., Pl. 49, Fig. 27c, *non* a, e (= *C. massiliense var. massiliense* and *var. carriense*).

Mentioned with illustration as *C. macroceros var. crassa* by: Nel (1968).

C. tripos macroceras var. tenuissima Karsten (1907): 411, Pl. 49, Fig. 28a–e.

Mentioned without illustration as *C. macroceros var. tenuissima* by: Nel (1968).

C. tripos scoticum Schütt (1892): 266, 302, e.p., Fig. 76 IVc *non* Fig. 91 IV (unidentifiable with certainty—Jörgensen (1911) considered it as possibly *C. intermedium* (Jörg.) Jörg. = *C. tenue*).

Non C. tripos macroceras f. scotica: Schröder (1900): 15, Pl. 1, Fig. 17g (= *C. massiliense var. massiliense*).

C. tripos: Bergh (1882): 204, e.p., Pl. 14, Fig. 27; Hensen (1887) p.p., Pl. 6, Fig. 58; *non C. tripos* (Müller) Nitzsch.

C. ostenfeldii Kofoid (1907b): 305, e.p., Pl. 26, Fig. 24, *non* 22, 23, 25 (= *C. massiliense var. massiliense* and *var. carriense*).

C. hundhausenii: Pavillard (1931): 92, Pl. 3, Fig. 7; *non C. hundhausenii* Schröder (= *C. massiliense var. carriense*)

? *C. macroceros subsp. gallicum f. californiense* (Kof.) Jörgensen (1911): 64, Pl. 7, Figs. 136, 137; (1920): 89, Fig. 80 (all solitary heteromorphs); Forti (1922): Pl. 3, Fig. 49 (= Jörgensen Fig. 137).

? *C. macroceros f. californiense:* Halim (1960): 180, Pl. 5, Fig. 6 (solitary heteromorph).

? *C. californiense* Kofoid (1907b): 302, Pl. 23, Figs. 6–9; (1908a): 380, 382, Figs. 32, 33; Karsten (1907) Pl. 51, Fig. 15 (all solitary heteromorphs); Pavillard (1931): 88, Pl. 3, Fig. 2 (long horned cell).

? *Non C. macroceros var. hainanensis* Nie (1936): 62, Fig. 28A, B (? = *C. deflexum f. sinensis* Rein.).

Diagnosis: In the specimens examined, *C. macroceros* differs from *C. massiliense var. massiliense* (Gour.) Kars. and most specimens of *C. massiliense var. carriense* (Gour.) Rein. in that the ratio $\frac{B}{H}$ is $\geqq$ 0,90 (the single specimen of *C. macroceros* recorded from the Agulhas current in which this ratio was 0,83, differed from

C. massiliense in that the girdle diameter was 51 μ); *C.* macroceros differs from the few specimens of *var. carriense* in which the ratio $\frac{B}{H}$ is $\geq$ 0,90, but always $<$ 1,50, in that the right horn MRC is generally $>$ 10° and the sum of left and right horn MRC's is generally $>$ 25°; *C. macroceros* differs further from those specimens of *var. carriense* in which the ratio $\frac{B}{H}$ is $>$ 1,10, in that the difference between the left horn radius co-ordinates of the tangent, parallel to the girdle, to the lower edge of the antapical horn and of the point of MBC is $<$ 100 μ, mostly $<$ 50 μ; (the three specimens of *C. macroceros* recorded in which the right horn MRC was $\leq$ 10°, differed from *var. carriense* in that in the first, the ratio $\frac{B}{H}$ was 2,20, in the second the sum of left and right horn MRC's was 36° and in the third, girdle diameter was 54 μ).

C. macroceros differs from *C. deflexum* (Kof.) Jörg. in lacking a marked ventral deflexion of the antapical horns; in terms of polar co-ordinate measurements of two-dimensional camera lucida drawings, *C. macroceros* differs from *C. deflexum f. deflexum* in that the left horn MRC often occurs beyond the 75 μ radius co-ordinate; those specimens of *C. macroceros* in which the left horn MRC occurs before the 75 μ radius co-ordinate, differ from most specimens of *f. deflexum* in that the left horn degree co-ordinate with the 105 μ radius co-ordinate is $<$ 150°, mostly $<$ 145°; (the single specimen of *C. macroceros*, recorded from Oslo Fiord, in which this co-ordinate was 152° differed from *f. deflexum* in that the difference between left and right horn MBC degree co-ordinates was 7°); *C. macroceros* differs from those specimens of *f. deflexum* in which the left horn degree co-ordinate with the 105 μ radius co-ordinate is $<$ 150°, in that the right horn degree co-ordinate with the 105 μ radius co-ordinate is $<$ 115° *and* the difference between the left and right horn MBC degree co-ordinates is $\leq$ 20°; (the two specimens recorded of *C. macroceros* in which this difference was $>$ 20°, (Abé (1920) Fig. 47c and Karsten (1907) Pl. 49, Fig. 27c), differed from *f. deflexum* in that the left horn degree co-ordinate with the 105 μ radius co-ordinate was $<$ 135° and the right horn degree co-ordinate with the 105 μ radius co-ordinate was $<$ 100°). *C. macroceros* differs from *C. deflexum f. deflectomassum* Rein. in that the ratio $\frac{L90}{D}$ is $\geq$ 0,90 and the difference between left and right horn MBC degree co-ordinates generally $\leq$ 20°; *C. macroceros* differs from *C. deflexum f. sinensis* Rein. in that the difference between left and right horn MBC degree co-ordinates is generally $\leq$ 20° and the sum of left and right horn MRC'S is often $<$ 45°; (the two specimens recorded of *C. macroceros* in which the difference between the left and right horn MBC degree co-ordinates was $>$ 20°, differed from *f. sinensis* in that in the one, the sum of left and right horn MRC's was 31°, in the other the right horn MBC radius co-ordinate was $<$ 60 μ and the girdle diameter about 53 μ). *C. macroceros* differs further from *C. deflexum* in that far coarser and more prominent denticles or spines may occur along the lower margins of the antapical horns in the region of recurvature, than are ever found in *C. deflexum*, and the girdle is often incompletely developed on the right side.

C. macroceros generally differs from *C. trichoceros* (Ehb.) Kof. in that the left horn MBC degree co-ordinate is $< 70^\circ$; the few specimens of *C. macroceros* in which this co-ordinate is $\geq 65^\circ$, differ from the few specimens of *C. trichoceros* in which this co-ordinate is $\geq 65^\circ$, in that the girdle diameter is $\geq 55\ \mu$, while in the specimens of *C. trichoceros* it is $\leq 45\ \mu$.

C. macroceros differs from *C. tenue* O. & S. in that the left horn degree co-ordinate with the 15 μ radius co-ordinate is $< 70^\circ$.

INTRODUCTION

C. macroceros is one of the commonest and most widespread species of Section *Macroceras* and yet the overall picture of its variation and distribution is not complete. It has been confused with *C. deflexum* and this is discussed under that species. It exhibits a variation in form correlated with a variation in temperature. Previous authors have regarded the warm water form as a discrete taxon. Sournia (1966) treated it as a variety, *var. gallicum* (Kof.) Sournia. Peters (1932) was the first to refer to it as a variety, but apparently unintentionally, as "die *var. gallicum* Kofoid." Similarly, Schiller (1937) referred to "*var, gallicum* (Kofoid) Jörg." and Halim (1963) to "*f. gallicum* (Kof.) Jörg."

Jörgensen (1911) considered '*C. macroceros subsp. gallicum* (Kof.) Jörg.' to differ from *subsp. macroceros* in being somewhat smaller and more delicate, with the right side of the girdle frequently indistinct or incompletely formed, the thecal structure usually not apparent, sometimes distinct in older specimens but much less developed than in *subsp. macroceros*, the antapical horns initially less divergent, their recurvature almost angular and the angle made by the forward recurvature of the right horn more or less smaller than 90°, (being mostly 90° or a little larger in *subsp. macroceros*). Graham & Bronikowsky (1944) noted that the body was longer in forms from the cold North Atlantic. Jörgensen gave the girdle diameter of *subsp. macroceros* as 48–57 μ and of '*subsp. gallicum*' as 45–55 μ, exceptionally up to 70 μ. He commented: "there is no character by which these two forms can be absolutely separated".

An examination of the range of form occurring in *C. macroceros* indicates that it is indeed impossible to divide this species into infraspecific taxa which are always distinct.

The cold water form was originally described from the Baltic, the warm water form from off San Diego, California. In the Agulhas current NGY samples, with one exception, only specimens resembling Kofoid's iconotype were found, but with the girdle incompletely formed and invisible plate sutures. The exception was a recently divided specimen from station NGY 41 (temperature from 50–0 m, 16,66–17,49°C, see p. 352), with a girdle diameter of 51 μ,

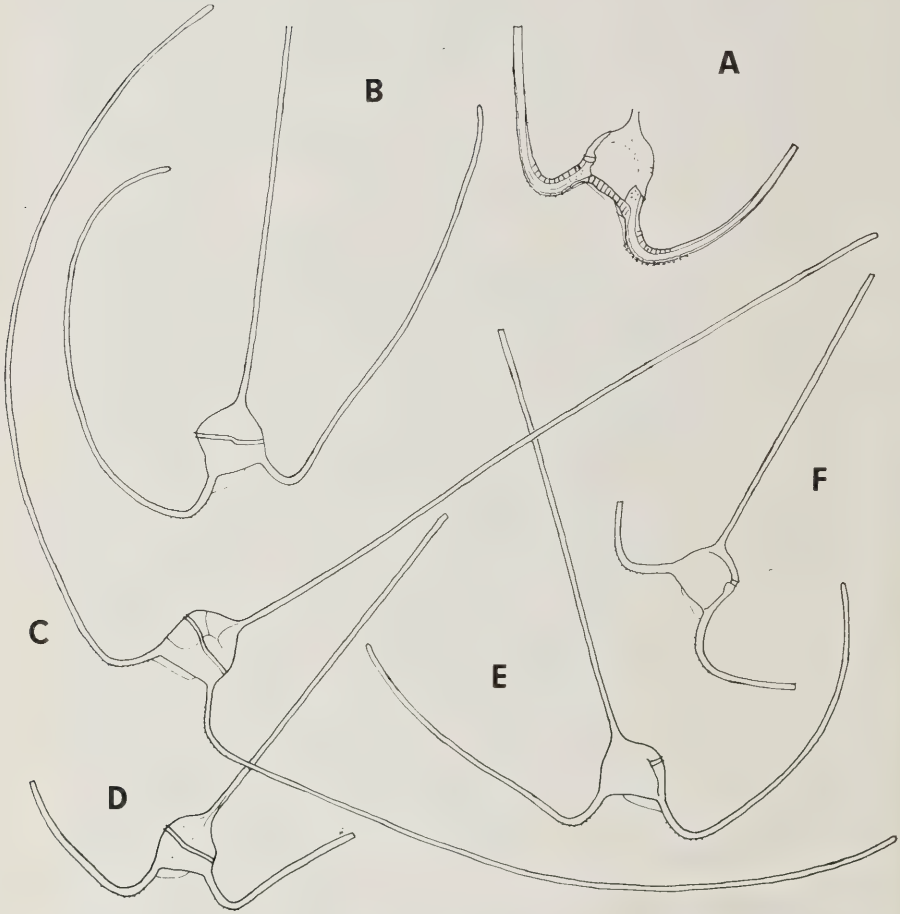

Fig. 1.
C. macroceros (Ehb.) Vanh.: Specimens from Agulhas current NGY stations. Girdle diameters: **A** 51 μ, **B** 48 μ, **C** 48μ, **D** 40 μ, **E** 45 μ, **F** 45 μ; **A,** recently divided specimen from station NGY 41 with thickened theca, thecal wall shown in optical section and surface view.

and a posterior half in which the theca was well developed with thickened walls and prominent spines supporting narrow lists along the lower margins of the antapical horns in the region of recurvature. (See Fig. 1).

Specimens were also examined from an NIOE station further South, NIOE 121 (40° 02′ S, 29° 28′ E, temperature from 100–0 m, 12,15–13,70 C, Shipley & Zoutendyk 1964) and from Oslo Fiord, (see Figs. 2 and 3). Relevant measurements of body size and antapical horn curvature of these specimens and of the iconotypes of Claparéde & Lachmann (1859) and Kofoid (1907b) are shown in Figure 4.

In the Oslo specimens, the thecal wall is well developed with fairly coarse spines on the lower margins of the distal parts of the antapical horns, but the girdle is often incompletely formed on the right side; the left horn MRC occurs between the 60 and 105 μ radius co-ordinates and the antapical horns are recurved forwards in a rounded curve, the girdle diameter is mostly 54–63 μ and the ratio body length/girdle diameter is mostly greater than 1,20. In the NGY specimens, the thecal wall is more delicate, the antapical horns thinner, usually with minute spines in the region of recurvature, the left horn MRC occurs between the 30 and 60 μ radius co-ordinates, and the antapical horns are recurved forwards in an angled curve; the girdle diameter is mostly 42–48 μ and the length/breadth ratio does not exceed 1,20. There is no difference in the initial divergence of the antapical horns between specimens from the two localities. The angle made by the forward recurvature of the right horn usually approximates a "rounded" right angle in the Oslo Fiord specimens, and an "angled" right angle in those from the Agulhas current.

The NIOE specimens are in all respects intermediate in character between those from the Oslo Fiord and from the NGY Agulhas current samples, making it impossible to place the three groups of specimens in anything but the same taxon.

Distribution and variation as described in the literature: Ocean currents and their seasonal variation complicate an investigation of the distribution of planktonic taxa which vary morphologically with temperature changes, but an examination of the literature indicates that the differences between the cold and warm water forms of *C. macroceros*, with regard to both morphological variation and distribution with reference to temperature, are not clear cut, and that the species varies more than indicated in Jörgensen's description of 1911.

Jörgensen gave the girdle of the cold water '*subsp. macroceros*' as 48–57 μ and mentioned that the diameter of the warm water '*subsp. gallicum*' was exceptionally as much as 70 μ. The available evidence indicates that larger diameters are found in specimens outside the tropics. Diameters in excess of 60 μ and up to 70 μ have been recorded in specimens from the Atlantic and

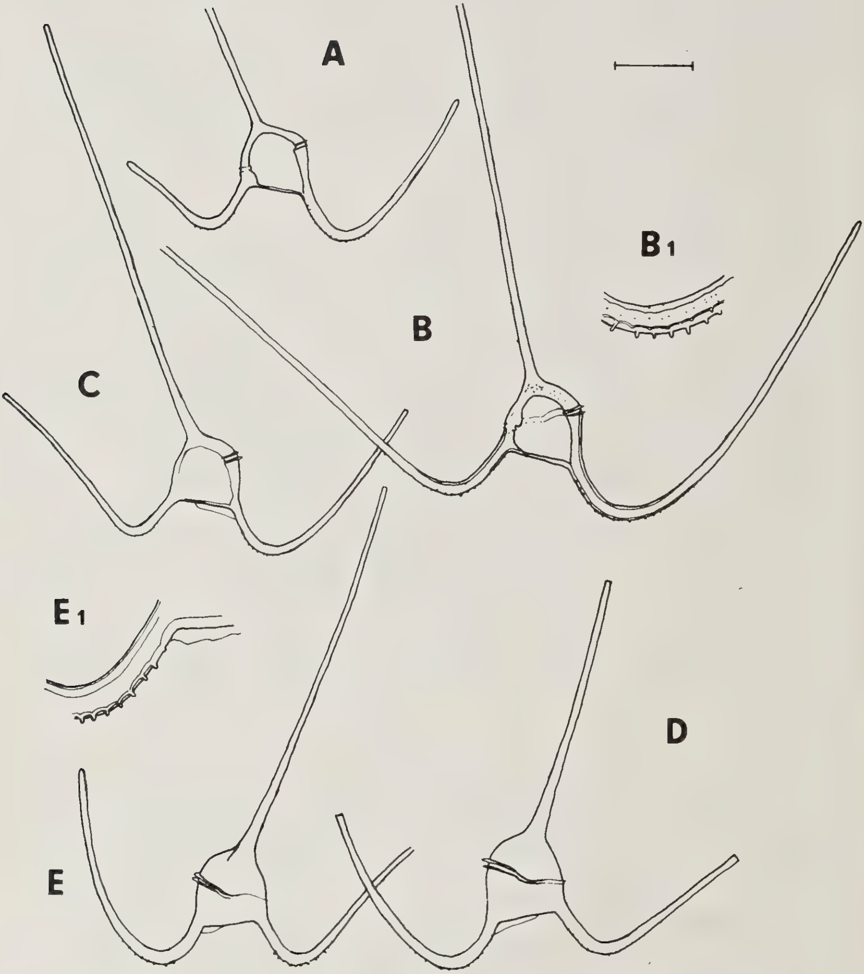

FIG. 2.
C. macroceros (Ehb.) Vanh.: Specimens from S.W. Indian Ocean station NIOE 121. In **B**, thecal wall seen in surface view and optical section; scale line represents 50 μ; **B1** and **E1**, details of portion of left horn at a higher magnification, thecal wall shown in optical section.

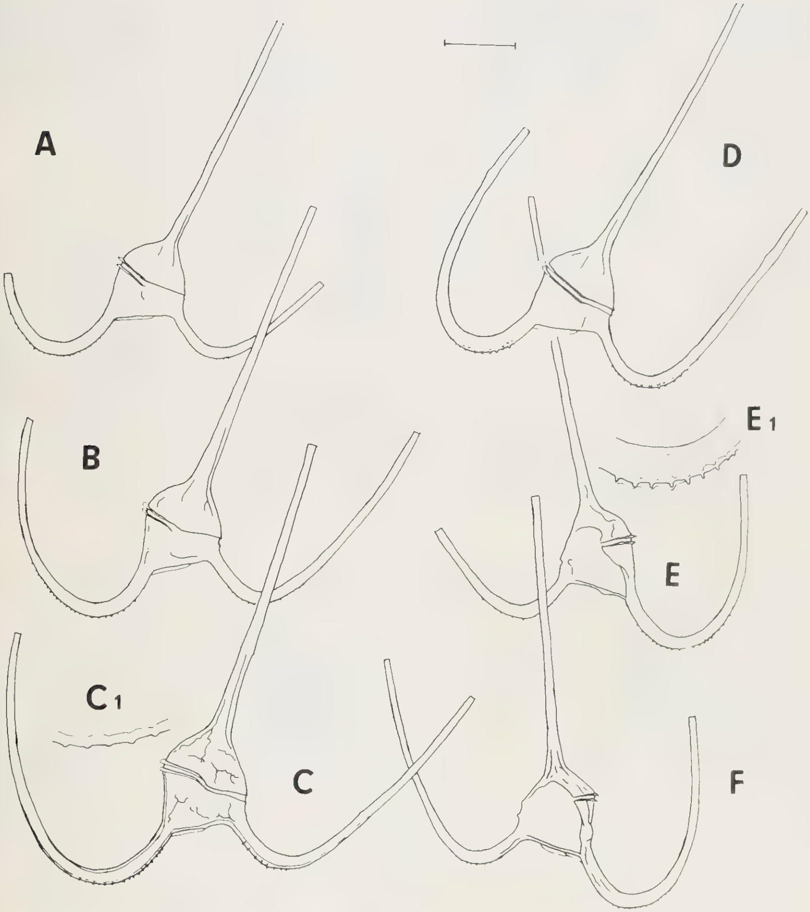

FIG. 3.
C. macroceros (Ehb.) Vanh.: Specimens from Oslo Fiord. In **C,** thecal wall seen in optical section and surface view; scale line represents 50 μ; **C1** and **E1,** details of portion of left horn at a higher magnification, thecal wall in optical section.

adjacent waters: from Oslo Fiord, the Shetland Isles (Vanhoeffen 1897*), near the Azores (under the name *C. hundhausenii*, Pavillard 1931*, treated as '*var. gallicum*' by Schiller, 1937), from Vigo (Margalef & Duran 1953) and the Mediterranean (Paulsen 1930, Rampi 1939*).

In the S. Atlantic, Peters reported both gigantic robust cells and delicate thin walled cells, the distribution of which showed no definite pattern. He found only robust forms in his "Transition area" (S. central Atlantic, between 37 and 45° S.). In the Indian ocean, two robust specimens, from an unspecified locality, presumably a cold water southern station, are depicted by Karsten (1907, Pl. 49, Figs. 27b and c, diameters estimated at 68 and 88 μ). In the Pacific and adjacent waters, large specimens are recorded from Mutsu Bay (Abé 1927, diameter 50–68 μ) and off San Diego (Kofoid 1907b, under the name *C. ostenfeldii*).

The highest values of the ratio $\frac{B}{H}$, in excess of 1,50, appear to be found in specimens from cooler waters, where, however, ratios of less than 1,00 are also recorded.

Graham (1941), who considered that there were no truly temperate oceanic ceratia, described '*C. macroceros subsp. macroceros*' as a subpolar taxon. This is misleading, for it implies a far greater difference between the cold and warm water forms of *C. macroceros* than exists. In fact, Sournia (1967) considered Graham & Bronikowsky's specimen of '*subsp. macroceros*' from S.E. of Greenland (1944, Fig. 21F) to be intermediate between '*var. macroceros*' and '*var. gallicum*'.

Atlantic ocean: In the Atlantic there appears to be no discontinuity in the variation, but a gradual change in appearance associated with a change in temperature. Pavillard (1931) wrote of '*subsp. gallicum*': "Remplace le type dans le mers tempérés et chaudes, sans qu'il soit possible de tracer une démarcation territoriale absolue". Graham & Bronikowsky found, with two exceptions, that '*subsp. macroceros*' was only recorded from Carnegie N. Atlantic stations North of latitude 40°, while Mangin recorded what he named as *C. macroceros* from 25–77°N. The three specimens he figures have the ratio $\frac{B}{H}$ of about 1,80–1,86. Silva (Bay of Cascais, 1949) and Margalef & Duran (Vigo, 1953) found both what they considered to be '*subsp. gallicum*' and '*subsp. macroceros*' in Iberian Atlantic waters. One of the specimens depicted by Silva (l.c. Pl. 9, Fig. 11) resembles specimens from NIOE 121, except that the distal parts of the antapical horns are less spreading. Margalef & Duran gave the diameter of '*subsp. gallicum*' (l.c. Fig 12c–e) as 45–53 μ, and of the form "Quiza . . . corresponde al tipo de la especie" (l.c. Fig. 12a, b) as 54–70 μ. The specimen in Fig. 12b is intermediate in character between the specimens of Figs. 12a and 12c.

Jörgensen (1911) published two figures of '*subsp. macroceros*' from Bergen,

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* Calculated from scale of figure.

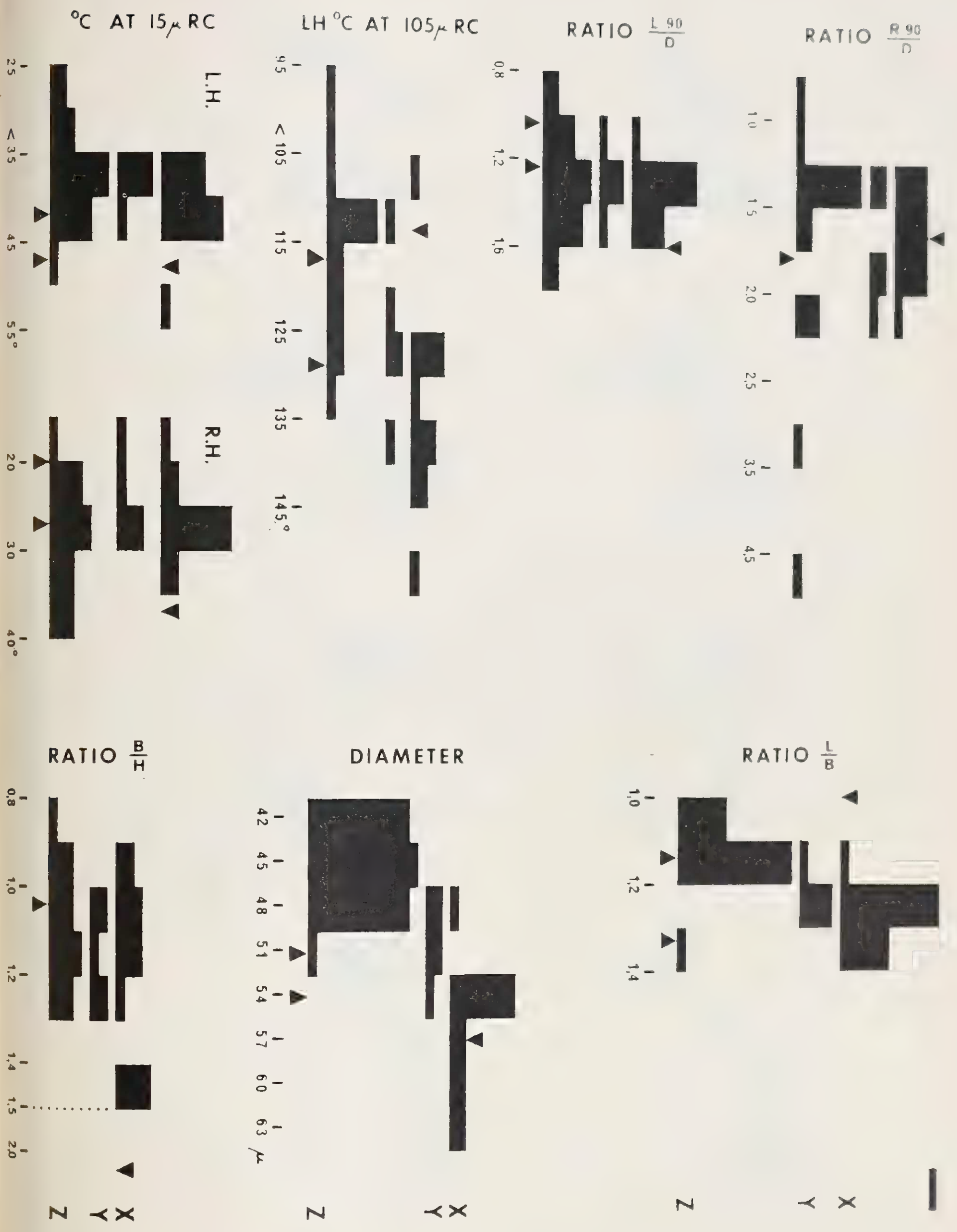
°C AT 15μ RC
L.H.
25
< 35
45
55°
R.H.
20
30
40°
LH °C AT 105μ RC
95
< 105
115
125
135
145°
RATIO L 90/D
0,8
1,2
1,6
RATIO R 90/D
1,0
1,5
2,0
2,5
3,5
4,5
RATIO B/H
0,8
1,0
1,2
1,4
1,5
2,0
DIAMETER
42
45
48
51
54
57
60
63 μ
RATIO L/B
1,0
1,2
1,4
X
Y
Z

Fig. 4A

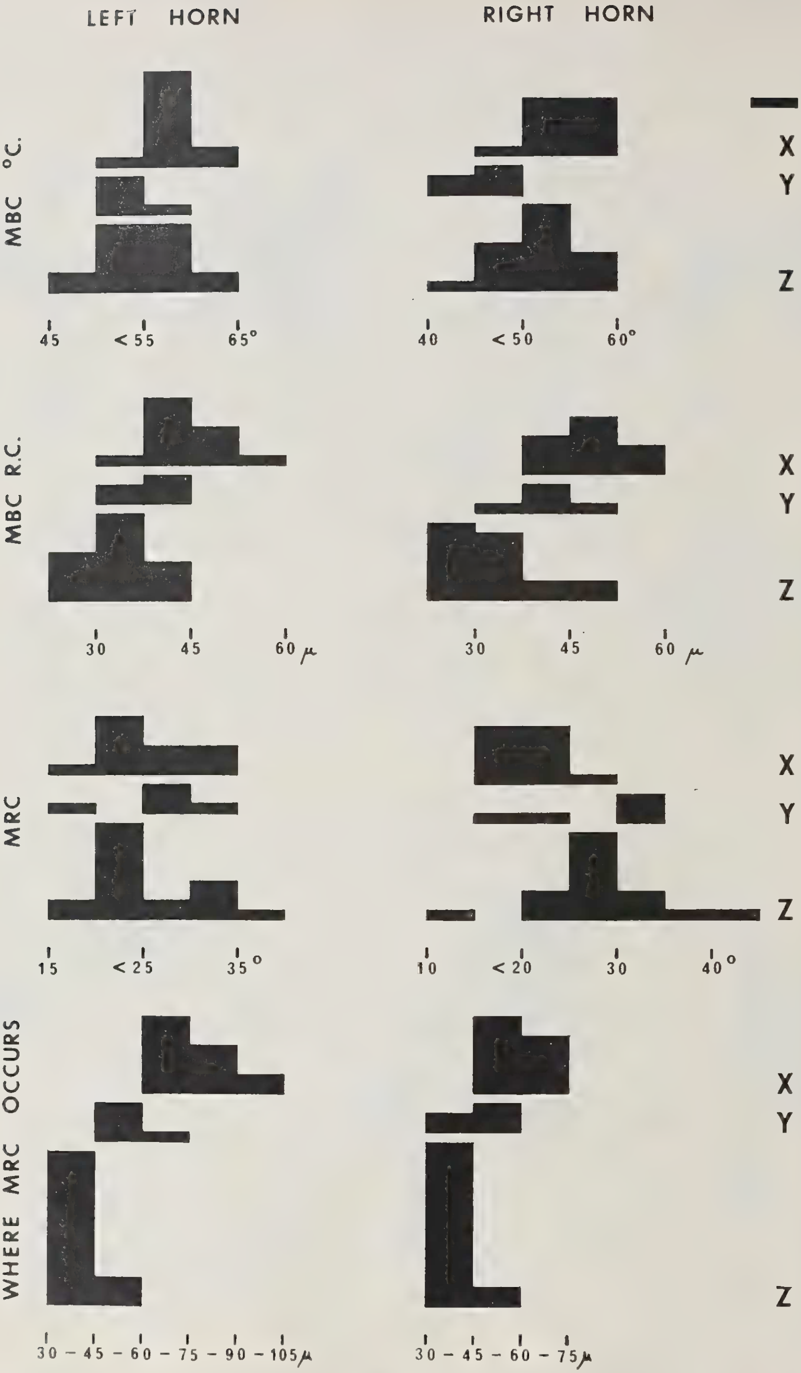
LEFT HORN
RIGHT HORN
MBC °C.
45
< 55
65°
40
< 50
60°
MBC R.C.
30
45
60 μ
30
45
60 μ
MRC
15
< 25
35 °
10
< 20
30
40 °
WHERE MRC OCCURS
30 – 45 – 60 – 75 – 90 – 105μ
30 – 45 – 60 – 75μ
X
Y
Z
X
Y
Z
X
Y
Z
X
Y
Z

Fig. 4B

one of which (l.c. Fig. 133) agrees well with a figure of Bergh (1882), reproduced in Paulsen's "Peridiniales" (1908) as *C. macroceros*, the other with an incomplete girdle, (l.c. Fig. 132a) is in many respects intermediate between Fig. 133 and a figure of a specimen of '*subsp. gallicum*' from the Azores (l.c. Fig. 135).

The only figure of a specimen from the S. Atlantic appears to be that of Peters (1932), from a station off Cape Town, with an incomplete girdle, which resembles Kofoid's iconotype, but which Peters did not appear to recognise as such, describing it as a fairly distinctive form of *C. macroceros* characteristic of his "Agulhas area", although he had commented: "In dem Expeditionsgebiet wurde überweigend die *var. gallicum* Kofoid angetroffen; nur im Süden . . . (between about 35 and 45°S) . . . wurden vornehmlich der Hauptform ähnliche Vertreter gefangen." He commented on the great variability of the species, and found it to be absent from his "Falkland area".

Mediterranean: Jörgensen (1920) considered that only '*subsp. gallicum*' was present in the Mediterranean. Pavillard (1907) had, however, written of specimens from the Gulf of Lyons: "parfaitement identiques au dessin classiques de Bergh". Forti (1922) reported specimens somewhat similar to Jörgensen's Fig. 132, and Böhm (1931a) noted that in the Adriatic '*subsp. gallicum*' "nahert sich oft betrachtlich der Hauptart". Paulsen (1930) found forms of '*subsp. gallicum*' with incomplete girdles and more robust forms with complete girdles in the Alboran Sea. In his figure of the latter, which Sournia (1967) considered to be intermediate between '*var. gallicum*' and '*var. macroceros*', the forward recurvature of the antapical horns is not angled. Rampi (1939) published a poor figure of '*var. gallicum* (Kof.) Jörg.' in which the girdle is complete, the forward recurvature of the antapical horns rounded, and the estimated diameter about 63 μ. The Travers (1962), in their account of the phytoplankton of the Gulf of Marseille, listed the species as *C. macroceros*, not differentiating '*var. gallicum* (Kof.) Jörg.'.

Indian Ocean and Australian Waters: Wood (1954) recorded both '*subsp. macroceros*' and '*subsp. gallicum*' from Australian waters, but his concept of the former appears to be confused, for the specimen illustrated has the ratio $\frac{B}{H} < 0{,}80$ (and is probably a specimen of *C. massiliense*), and he described its

Fig. 4A, B.

C. macroceros (Ehb.) Vanh.: A comparison of antapical horn curvature measured in polar co-ordinates, diameter and the ratio $\frac{L}{B}$, in specimens from Oslo Fiord (X), S.W. Indian Ocean station NIOE 121 (Y) and Agulhas current NGY samples (Z). LH °C left horn degree co-ordinate, RC or R.C. = radius co-ordinate, L.H. and R.H. = left and right horns = $\frac{L}{B}$ length of body measured from base of outer edge of left horn to base of apical horn/girdle diameter. For other abbreviations, see text. The triangle above the X histograms indicates the measurements for the specimen in Claparéde & Lachmann's iconotype, (enlarged assuming a girdle diameter of 57 μ), the triangles with the Z histograms indicate the measurements of the specimens in Kofoid's iconotype. The isolated black bar indicates one specimen.

distribution as "... Rarer in tropical waters, where it is replaced by *C. gallicum*". In his Indian Ocean Checklist (1963), he treated *C. gallicum* as a separate species and it is unlikely that his records for *C. macroceros* refer to the cold water form, for they are all from relatively warm waters, and some, eg. Ballantine (1961), refer wholely or in part to other species. The variation of *C. macroceros* in the S.W. Indian ocean as far South as latitude 40°, has been discussed. The only other records of forms from the Indian Ocean resembling cold water N. Atlantic forms, are the previously mentioned robust specimens depicted by Karsten (1907, Pl. 49, Figs. 27b and c). Steemann Nielsen recorded only '*subsp. gallicum*' in the Dana Indian ocean samples, but these did not extend South of latitude 36°. He described this taxon as "one of the most frequent ceratia, interoceanic, tropical-subtropical euphotic".

Pacific Ocean and East Asian waters: The only specimen of *C. macroceros* depicted in the literature from this area, which resembles Claparède & Lachmann's iconotype of the cold water form of *C. macroceros*, is that of Wang (1936) from the Gulf of Pê Hai (Gulf of Chili). Wang gives a diameter range of 43–48 μ, which is lower than given by Jörgensen, but in the specimen illustrated, the girdle is completely formed, the thecal wall is thickened with ridges, the antapical horns are coarsely toothed and recurved forwards a in rounded curve, the ratio body length/breadth is about 1,24 and the ratio $\frac{B}{H}$ about 1,93. Sournia (1967), however, considered this to be intermediate between '*var. gallicum*' and '*var. macroceros*'. Böhm (1931b) recorded *C. macroceros* from off the Eastern coast of Asia as "rather uncommon as *subsp. gallcium*" from a few stations South of latitude 25°. The specimen illustrated has a complete girdle and resembles Paulsen's Fig. 54A from the Mediterranean.

Specimens from Mutsu Bay, Japan, exhibiting a considerable range of variation are depicted by Abé (1927). Thecal structure is not shown, the girdle is mostly incomplete, diameter varies from 50–68 μ, the ratio body length/breadth is about 1,16–1,21, the ratio $\frac{B}{H}$ about 1,08–1,50 and the spread of the antapical horns is very variable. Forms with spreading horns, which most resemble Kofoid's iconotypes in horn curvature, were named *C. macroceros*, those with less spreading horns, the curvature of which in some instances resembled specimens referred to by other authors as '*subsp. macroceros*', were named '*subsp. gallicum*', and a form with a swollen body was named '*C. macroceros var. karstenii*', which Abé considered to be the same as Karsten's '*C. tripos var. crassa*' (1907, Pl. 49, Fig. 27e), here treated as *C. massiliense*. Sournia (1967) considered the specimens referred to by Abé as *C. macroceros* to be intermediate between '*var. gallicum*' and '*var. macroceros*'.

Steemann Nielsen (1934) recorded only '*subsp. gallicum*' from the Dana S. Pacific stations, where it was not observed in cold waters S.E. of New Zealand and in truly neritic stations. He noted a slight tendency for the diameter to increase with a decrease in temperature. For example, at a station with a surface temperature of 26,9°C, only diameters of 42–45 μ were recorded, while at a station with a surface temperature of 21,0°C, diameters of 46–55 μ were recorded.

Graham & Bronikowsky (1944) recorded only '*subsp. gallicum*' from the N. Pacific Carnegie stations, where the N. limits were between latitudes 38 and 42°. They considered the absence of '*subsp. macroceros*' from the cold N. Pacific as indicative of the hydrological isolation of this part of the ocean. This again suggests a far greater difference between the cold and warm water forms of *C. macroceros* than is evident. They also noted that at most of the cold N. Pacific stations, the phosphate content of the water was generally above 100 mg PO_4/m^3, while in the cold N. Atlantic samples where '*subsp. macroceros*' was found, the phosphate content was mostly below 50 mg/m^3, and further, that '*subsp. gallicum*' was absent off Peru, where again the phosphate content was high. This factor appears to be more significant than they indicated. They considered that in the cold S. Pacific (the Southernmost Carnegie station being at about latitude 40°) "the species assumed the aspect of *subsp. macroceros*", but the specimen figured (l.c. Fig. 21C) most resembles *C. deflexum f. deflectomassum*—it has the ratio $\frac{B}{H}$ about 0,56.

Hasle (1969) recorded *C. macroceros* from the Pacific Southern Ocean, but made no mention of its appearance.

The foregoing shows that, while the extreme warm and cold water forms of *C. macroceros* are recognisable, the presence of a continuous series of intermediates makes it impossible to divide the species into definable supspecific categories of even the lowest rank, and accordingly the infraspecific taxa of *C. macroceros* are discarded.

Culture experiments on the effects of phosphates and of temperature on forms from cold and warm waters would be of great interest. Also, more records of occurrence and variation of the species in cold Southern waters are needed.

Description

Thecal ornamentation: The girdle is often incompletely formed on the right side: seen dorsally, about halfway across the upper and lower girdle lists become smaller, so that on the right side they are reduced to ridges or are altogether absent, or only the upper list is present as a ridge; seen ventrally, on the right side of the sulcus the girdle is absent or very faintly indicated. Incomplete girdle development is more usually found in truly warm water specimens, and was the case in all Agulhas current specimens seen, but it is sometimes seen in specimens from cooler waters. In warm water specimens, the thecal walls are delicate and unridged, the antapical horns are slender and smooth, or with fine minute spines along the lower margins of the proximal parts; a single smooth margined to slightly serrated list is present between the base of the left and horn and the hypotheca, extending about two thirds of the way across the hypotheca base. In cold water forms, the theca is thickened and ridged, and the antapical horns are thicker with coarser spines, which sometimes support a narrow list.

Horn length and disposition: Cold water specimens are often found with broken (or autotomised?) antapical horns, as was the case in those seen from Oslo Fiord and station NIOE 121, where in most specimens the horns only extended to the 105μ radius co-ordinate, and in no instance beyond the 225 μ co-ordinate. In some of the Agulhas current NGY specimens, the antapical horns were long with tapered, rounded, sometimes slightly inflated, tips; in others, the horns were short, not exceeding the 105 μ radius co-ordinate, with rounded truncate, abruptly truncate, in two instances slightly inflated, tips. In specimens with short horns with rounded tips it was not possible to determine whether the horns were short *ab initio* or whether they were broken or autotomised. Spread of antapical horns is variable, regardless of temperature, but truly cold water forms have not been recorded with as great a spread as sometimes seen in those from warm waters, and in cold water specimens the recurved distal part may lie roughly parallel to the apical horn. When the antapical horns are long, the ends appear to be slightly flexible, sometimes curving outwards. The bases of both antapical horns make an obvious angle with the base of the hypotheca. In typical warm water specimens, the forward recurvature of the more slender antapical horns is generally "angled", while in typical cold water specimens with thicker horns, it is "rounded".

Jörgensen (1911) wrote of the cold water '*subsp. macroceros*' that the right horn was "stark ventral gerichtet". This was not observed in specimens examined under the microscope, nor shown by Abé (l.c. Fig. 47B) in figures of apical and antapical views.

Mangin (1912) depicted a specimen in which the distal part of the apical horn was inflated.

Polar co-ordinate measurements of horn curvature: Left horn: degree co-ordinate with 15 μ radius co-ordinate 27–60°, mostly 35–50°, not recorded above 50° in truly warm water forms; degree co-ordinate with 105 μ radius co-ordinate variable, 88–152°, mostly 105–145°; with 150 μ, 106–173°; with 300 μ, 128–197° in the few specimens seen with long horns; MBC degree co-ordinate 45–68°, mostly 50–60°; MBC radius co-ordinate 27–69 μ, mostly 30–60 μ, generally $< 38\ \mu$ in typical warm water forms and $> 38\ \mu$ in typical cold water forms and in the specimens with larger diameters figured by Paulsen (Alboran Sea, Mediterranean) and Abé (Mutsu Bay, Japan); MRC 10–35°, mostly 15–30°, occurring between 30 and 105 μ radius co-ordinates, (between 120 and 135 μ in Karsten's specimen, Pl. 49, Fig. 27c), generally before the 60 μ co-ordinate in typical warm water forms and beyond it in typical cold water forms, (between 30 and 75 μ

in Abé's specimens, and between 60 and 75 μ in those of Paulsen); $\frac{L90}{D}$ 0,90–1,80 (as much as 2,18 in a specimen figured by Karsten (1907) Pl. 49, Fig. 28a); $\frac{B}{H}$ 0,90–2,22 (0,83 in only one instance), generally not exceeding 1,30 in warm water specimens (1,08–1,55 in Abé's figures, 1,66 in Paulsen's Fig. 58C). *Right horn:* degree co-ordinate with 15 μ radius co-ordinate 17–45°, (zero in Karsten's Pl. 49, Fig. 27c), mostly 17–37°, generally less than in the left horn by up to 32° (52° in Karsten's Fig. 27c), mostly by 1–25°, sometimes greater than in the left horn by up to 10°; degree co-ordinate with 105 μ radius co-ordinate variable, 72–114°, mostly 80–110°; with 300 μ, 94–124° in the few specimens seen with long horns; MBC degree co-ordinate 33–62°, mostly 40–55°, less than in the left horn by up to 25° (30° in Karsten's Fig. 27c), mostly by 1–15°, sometimes greater than in the left horn by up to 5°; MBC radius co-ordinate 26–83 μ, mostly $<$ 42 μ in typical warm water forms and $>$ 42 μ in typical cold water forms (also in the specimens figured by Abé and Paulsen); less than in the left horn by up to 20 μ, mostly by up to 5 μ, or greater than in the left horn by up to 32 μ, mostly by up to 15 μ; MRC is 9–41°, mostly $>$ 20° in typical warm water forms and $<$ 23° in cold water forms (and the specimens figured by Abé and Paulsen); MRC occurs between 30 and 120 μ radius co-ordinates (between 15 and 30 μ in one small-diametered form), mostly between 30 and 45 μ in typical warm water forms, and beyond 45 μ in cold water forms (between 30 and 75 μ in Abé's specimens, and 45 and 75 μ in those of Paulsen); $\frac{R90}{D}$ 0,96–4,55, mostly 1,25–2,50; sum of right and left horn MRC's 23–69°, mostly 25–55°. (See Fig. 5.)

Dimensions: In specimens examined: From Oslo Fiord: girdle diameter 48–63 μ, mostly 54–63 μ; length hypotheca 30–42 μ; length epitheca 24–33 μ; angle made by intersection of projections of base of hypotheca and girdle 23–35°; length apical horn 168–294 μ. From NIOE station 121: girdle diameter 48–54 μ; length hypotheca 27–33 μ; length epitheca 18–27 μ; angle between hypotheca base and girdle 25–33°; length apical horn 228–300 μ. From Agulhas current NGY stations: girdle diameter 42–51 μ, mostly 42–48 μ; length hypotheca 24–30 μ; length epitheca 15–24 μ; angle between base of hypotheca and girdle 21–35°; length apical horn 138–525 μ. *From literature: Girdle diameter:* cold water forms 48–57 μ, warm water forms, including Mediterranean 45–55 μ, exceptionally up to 70 μ, (Jörgensen 1911); from Mediterranean, 58, 65 μ (Paulsen 1930); from off Vigo, Spanish Atlantic coast, 45–70 μ (Margalef & Duran 1953); S. Pacific 42–55 μ (Steemann Nielsen 1934); off San Diego 50–60 μ (Kofoid 1907b); Mutsu Bay, Japan 50–68 μ (Abé 1927); Gulf of Pê Hai (Gulf of Chili), China 43–48 μ (Wang 1936); Indian ocean, localities unknown, 65–68 μ (Karsten 1907)*, 88 μ (Karsten 1907, Pl. 49, Fig. 27c)*; Shetland Isles 68 μ (Vanhoeffen 1897)* off

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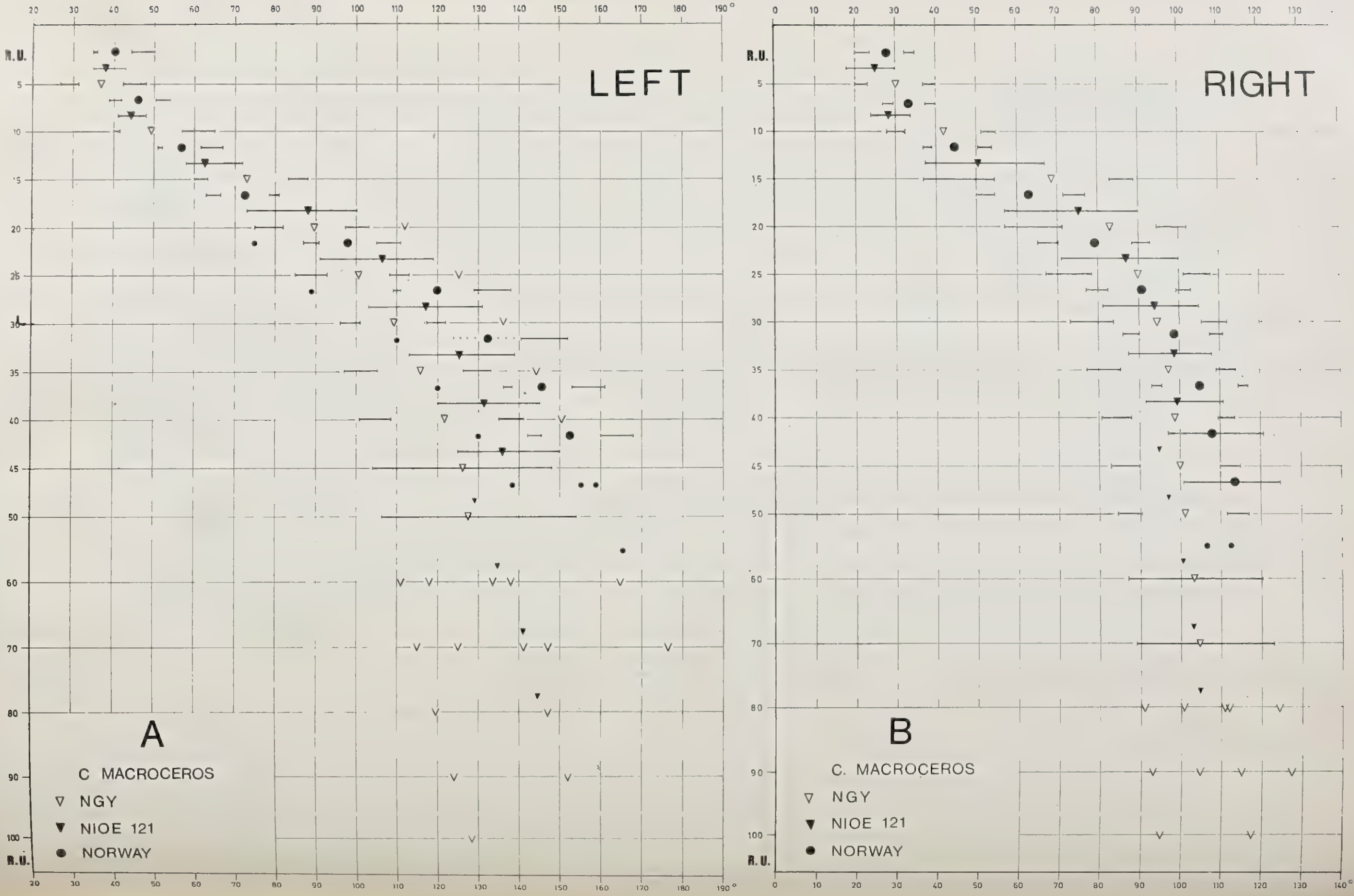
* Estimated from scale of figures.


LEFT
RIGHT
A
B
C MACROCEROS
▽ NGY
▼ NIOE 121
● NORWAY
C. MACROCEROS
▽ NGY
▼ NIOE 121
● NORWAY
R.U.
R.U.
R.U.
R.U.
5
10
15
20
25
30
35
40
45
50
60
70
80
90
100
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70
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190 °
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140 °

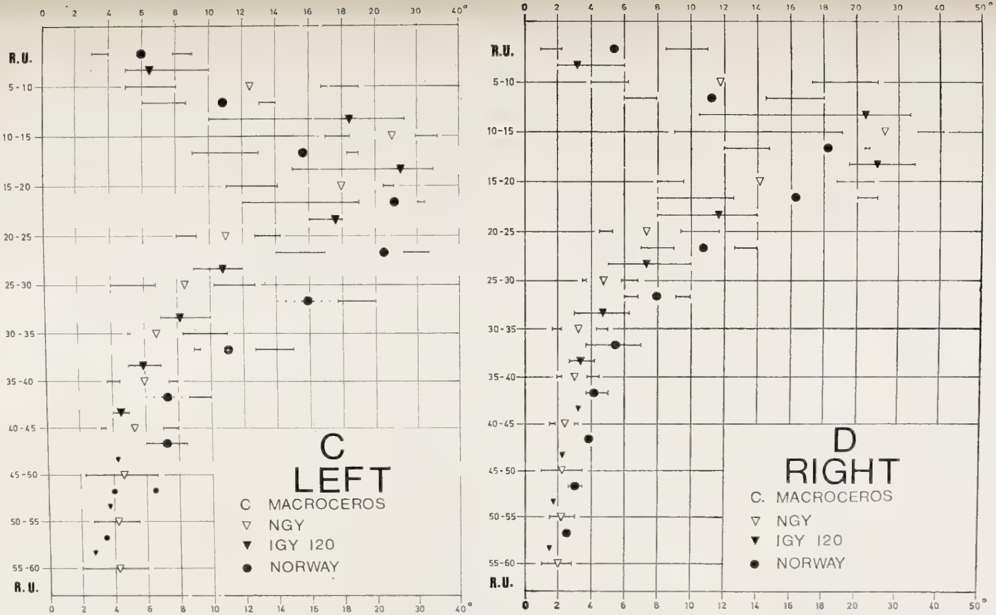

FIG. 5A–D.

C. macroceros (Ehb.) Vanh.: Antapical horn curvature in specimens from Oslo Fiord Norway, S.W. Indian ocean station NIOE 121, and Agulhas current NGY stations. **A**, curvature of left horn expressed in polar co-ordinates, that is, in degrees at intervals of 5 R.U. from 5 to 50 R.U., and at intervals of 10 R.U. from 50 to 100 R.U., (R.U. = radius unit, one radius unit is approximately equal to 3 μ); the symbols represent the mean degree co-ordinate value at successive 5 or 10 R.U. intervals for all specimens examined, the space between the thick transverse lines and the symbols indicates the Standard Deviation for each set of measurements, and the thick transverse lines indicate the range of measurements recorded beyond the limits of the S.D., or, where the S.D. was not calculated, the range of measurements recorded; where no measurements are recorded beyond the S.D., the S.D. is indicated by a dotted line; **B**, the same for the right horn; **C**, the rate of change of direction of curvature of the left horn, expressed in degrees over 5 R.U., from 5–10 to 55–60 R.U.; the symbols represent the mean rate of change in degrees over 5 R.U. for all specimens examined; **D**, the same for the right horn. The small symbols and V's represent single specimens.

Greenland 57 μ (Graham & Bronikowsky 1944)*. *Length apical horn* 270–400 μ (Jörgensen 1911).

The foregoing measurements do not apply to heteromorphic cells apparently belonging to this species, nor specimens referred to as '*C. californiense*' Kof.

THE PROBLEM OF '*C. californiense*' KOF. AND HETEROMORPHIC FORMS OF SECTION MACROCERAS

The occurrence of heteromorphic cells in *Ceratium* has been mentioned (Reinecke 1971). In Section *Macroceras* there appear to be four records of heteromorphic cells which may be identified with certainty as belonging to specific taxa.

In the first case, small heteromorphic cells appeared in a single cell culture of normal vegetative *C. tenue*† (Von Stosch 1964). The heteromorph was about one third of the girdle diameter of the normal vegetative cell, with a short apical horn, its length not much longer than that of the body, and straight, backwardly directed, short antapical horns, shorter than the girdle diameter, with closed rounded-tapered tips. In one instance a heteromorph was observed to undergo what appeared to be conjugation with a larger cell of normal vegetative appearance.

The second case (Steidinger & Williams 1970, Figs. 36c, d) is a record of a specimen (l.c. Fig. 36c) described as a "daughter cell" of a normal *C. trichoceros* cell (l.c. Fig. 36d). The heteromorph is 35 μ in diameter, with a long apical horn, about three times the length of the body, with antapical horns similar to those of the *C. tenue* heteromorph, and the right side of the body straight, almost truncated, in appearance.

The remaining two cases are two figures of two-celled chains of *C. macroceros*, (Jörgensen 1911, Fig. 6, from near Bergen, and Peters, fide Schiller 1937, Fig. 468b, locality not given). The anterior cell is the heteromorph, the posterior cell a typical vegetative cell. In all cells, the girdles are fully formed and the diameter of both cells in each chain is the same. Apparently, following the division of a normal vegetative cell, the parental anterior half has produced a daughter posterior half with short, backwardly directed straight horns in Jörgensen's specimen, and slightly longer, backwardly directed, but divergent, horns in that of Peters. In the heteromorphs, the tips of the antapical horns are tapered, almost pointed and closed, and in Jörgensen's specimen, the right side of the body is straight. The question of the nature of these heteromorphs is unsolved. Do the antapical horns continue growing, and eventually recurve forwards as is the case in typical members of Section *Macroceras?*

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* Estimated from scale of figures.

† Referred to as *C. horridum* (Cl.) Gran by Reinecke (1971).

If the antapical horns of the anterior cell in Peters' chain were to continue growing and eventually recurve forwards, the ratio $\frac{L90}{D}$ would be greater than that recorded for normal vegetative *C. macroceros* cells. Schiller (l.c. Fig. 468c) gives a second figure of Peters of a solitary heteromorph, with longer antapical horns with closed pointed ends, which are divergent and slightly curved, but show no recurvature forwards. Jörgensen (1911 Fig. 136) depicts a solitary heteromorph, from the Gibralter Straits, with similar slightly shorter antapical horns, the left one showing the beginning of a forward recurvature, which would give an estimated $\frac{L90}{D}$ of about 2,73. Halim (1963) figures in which a specimen both antapical horns have a forward recurvature, the left horn extending to just beyond the 90° co-ordinate, the right to just beyond the point of MBC; the horn tips are pointed and closed, the ratio $\frac{L90}{D}$ is about 2,00, the right horn MBC radius co-ordinate is about twice that of the left horn and the right side of the body is truncated.

Kofoid (1907b) published a new species *C. californiense* from off San Diego, illustrating three specimens, with complete girdles. In the first, (l.c. Pl. 23, Figs. 8,9), the apical horns are long, the right side of the body is truncated, the girdle diameter is about 35 μ, the antapical horns show a forward recurvature which does not reach the 90° co-ordinate, and the tips of the antapical horns are pointed and closed. A difference in thickness of the thecal wall at the base of all three horns indicated, according to Kofoid (1908a): "proximal growth . . . without preceding autotomy". The two other specimens (l.c. Figs. 6,7) have a diameter of about 45 μ short apical horns, a rounded right body profile, and short antapical horns with closed tapered tips, not exceeding the length of the girdle diameter, which are divergent and curve slightly. Whether or not all four specimens belong to the same species is debatable.

Pavillard (1931) depicted a specimen from off Portugal, which he named *C. californiense*, in which the girdle is apparently complete, the girdle diameter about 43 μ, the MBC radius co-ordinates long relative to the girdle diameter, the antapical horns are recurved forwards to a level beyond the top of the epitheca and are shown with truncated open ends, and the ratio $\frac{L90}{D}$ is about 2,33. A similar specimen from off Monaco is figured by Jörgensen (1911), but the antapical horns are shown, with open truncate tips, extending to about the point of MBC. Jörgensen considered *C. californiense* to be the front cell of a heteromorphic chain of *C. macroceros*, as all the heteromorphs he examined had newly formed posterior halves, which he termed "f. postico-juvenile", and named them "*C. gallicum f. californiense*" in the key to the figures. Pavillard, however, wrote of *C. californiense:* "constitue sûrement une especie autonome (contrà Jörgensen)."

Karsten (1907, Pl. 51, Fig. 15, under the name *C. californiense*, girdle diameter estimated at 52 μ) and Jörgensen (1920, Fig. 80, under the name *C. macroceros*

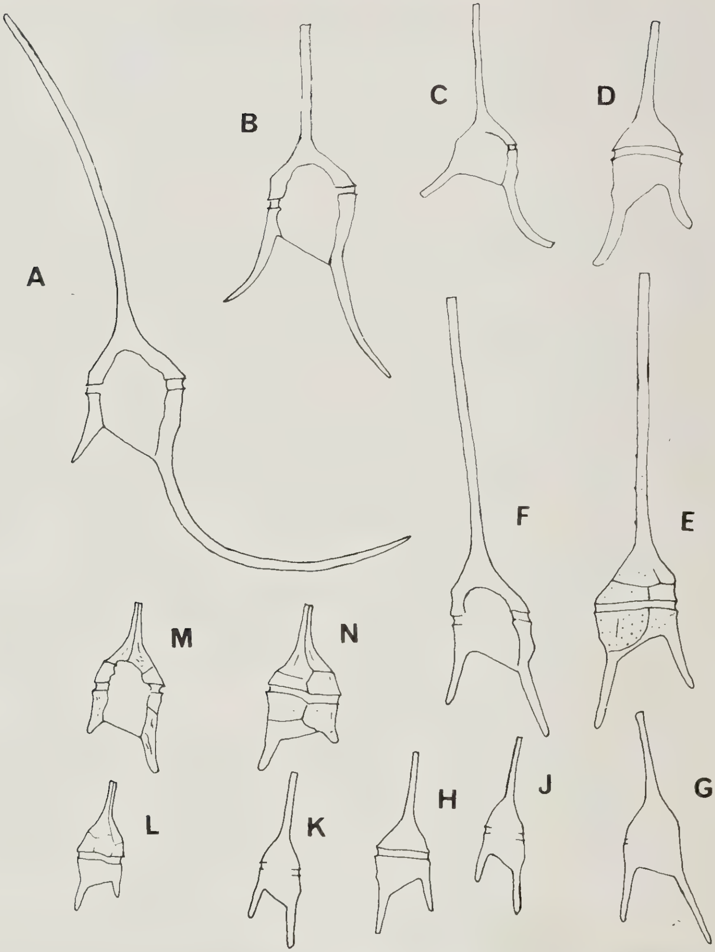


Fig. 6.

Heteromorphs of species of *Ceratium* found in samples from the Port Elizabeth line of NGY Agulhas current stations, (12 heteromorphs in 3 200 ceratium cells examined). Girdle diameters: **A** 45 μ, **B** 45 μ, **C** 33 μ, **D** 36 μ, **E** 39 μ, **F** 37 μ, **G** 27 μ, **H** 28 μ, **J** 23 μ, **K** 23 μ, **L** 23 μ, **M** 33 μ. **A** and **B** resemble to some extent, specimens referred to as '*C. macroceros*' or '*C. gallicum f. californiense*' by Schiller (1937) and Jörgensen (1911); **C** could be an unusually small form of *C. macroceros;* **E** and **F**, particularly **E**, resemble the heteromorph of *C. trichoceros* pictured by Steidinger & Williams (1970); **G** and **H** resemble to some extent the putative male gamete observed in a culture of *C. tenue* by Von Stosch (1964); **M** and **N** are ventral and dorsal views of the same specimen.

subsp. gallicum f. californiense, diameter estimated at 57 μ, and Fig. 92, under the name "*C.* (*horridum subsp.*) *buceros* Zach. a degenerate form answering to *f. californiense* (Kof.) of *C. macroceros subsp. gallicum*", diameter unknown) published figures of specimens with short slightly curved antapical horns similar to Kofoid's Figs. 6 and 7. In Jörgensen's specimens, the right profile of the body is truncated. For some unstated reason, Jörgensen considered Karsten's figure to belong to *C. deflexum*. The small spines along the lower edges of the antapical horns are, however, not typical of *C. deflexum*.

In the Agulhas current samples, a number of heteromorphs were seen, some of which resembled the small heteromorph of *C. tenue* recorded by Von Stosch, others the heteromorph of *C. trichoceros* photographed by Steidinger & Williams, one which resembled Jörgensen's Fig. 80, with a girdle diameter of 45 μ, and one in which the right horn was very short and the left horn was longer and recurved forwards to just beyond the 90° co-ordinate. In the latter, the diameter is 45 μ, the right side of the body truncated, the tips of the antapical horns pointed and closed, the ratios $\frac{L90}{D}$ 2,02 and $\frac{B}{H}$ 1,78 and the left horn MRC 8°, all outside the range of polar co-ordinate measurements recorded for specimens of *C. macroceros* from this area. This specimen cannot be regarded as belonging to *C. trichoceros* because the left horn MRC occurs between the 60 and 90 μ radius co-ordinates (over two successive 15 μ intervals) and the left horn MBC degree co-ordinate is 62°. (See Fig. 6.)

At this stage it is quite impossible to classify these heteromorphs unless they arise in single cell cultures of normal vegetative cells or are associated in chains with normal cells. Circumstantial evidence certainly suggests that for some reason, normal *C. macroceros* cells sometimes divide into two cells, of which the one with the parental anterior half produces a new posterior half with antapical horns, which, if fully developed, have for the size of the cell, somewhat longer MBC radius co-ordinates and a higher ratio $\frac{L90}{D}$ ($>$ 2,00) than normally found; the antapical horns are, however, often seen as short, straight and backwardly directed, or only slightly curved, with closed pointed tips.

Experiments to determine conditions under which heteromorphs are formed, their variation and whether or not they are involved in sexual reproduction would be very desirable.

It is of interest to note that Jörgensen (1920) found the heteromorph of Fig. 80 in the Sea of Marmora, apparently associated with conditions of low salinity.

Ceratium deflexum (Kofoid) Jörgensen (1911): 64, Pl. 7, Fig. 138.
Diagnosis: C. deflexum generally differs from all other taxa in this Subsection in exhibiting a ventral deflection of the antapical horns. In terms of polar co-ordinate measurements of two dimensional camera lucida drawings of the

specimens examined, *C. deflexum f. deflexum* and *C. deflexum f. deflectomassum* Rein. differ from *C. trichoceros* (Ehb.) Kof. in that the left horn MRC occurs before the 75 μ radius co-ordinate; *C. deflexum f. sinensis* Rein. differs from *C. trichoceros* in that the right horn MBC degree co-ordinate is $\leq 40°$.

C. deflexum differs from *C. massiliense* (Gour.) Kars. in that the sum of the left and right horn MRC's is $\geq 40°$; (*f. deflexum* and *f. deflectomassum* differ from the single specimen of *C. massiliense var. carriense* (Gour.) Rein. recorded in which the sum of left and right horn MRC's is $> 40°$ (Jörgensen (1911) Fig. 150a) in that the left horn degree co-ordinate with the 150 μ radius co-ordinate is $> 135°$; *f. sinensis* differs from this specimen in that the right horn MBC radius co-ordinate is $> 60\ \mu$).

F. deflexum differs from a number of specimens of *C. macroceros* (Ehb.) Vanh. in that the left horn MRC occurs before the 75 μ radius co-ordinate; *f. deflexum* differs from those specimens of *C. macroceros* in which the left horn MRC occurs before the 75 μ radius co-ordinate in that the left horn degree co-ordinate with the 105 μ radius co-ordinate is generally $\geq 150°$; (*f. deflexum* differs from the single specimen of *C. macroceros* in which this co-ordinate was 152° in that the difference between left and right horn MBC degree co-ordinates is $> 15°$); specimens of *f. deflexum* in which the left horn degree co-ordinate with the 105 μ radius co-ordinate is $< 150°$, differ from *C. macroceros* in that the difference between left and right horn MBC degree co-ordinates is $> 20°$ and/or the right horn degree co-ordinate with the 105 μ radius co-ordinate is $> 115°$; (*f. deflexum* differs from the two specimens of *C. macroceros* in which the difference between left and right horn MBC degree co-ordinates was $> 20°$, in that the degree co-ordinate with the 105 μ radius co-ordinate is $> 135°$ in the left horn and $> 100°$ in the right). *F. deflectomassum* differs from *C. macroceros* in that the ratio $\frac{L90}{D}$ is $< 0{,}90$, the left horn degree co-ordinate with the 105 μ radius co-ordinate is $> 135°$, the difference between left and right horn MBC degree co-ordinates is $> 20°$ and the ratio $\frac{B}{H}$ is generally $< 0{,}90$. *F. sinensis* differs from *C. macroceros* in that the difference between left and right horn MBC degree co-ordinates is $> 20°$ *and* the sum of left and right horn MRC's is $> 45°$ *and* the right horn MBC radius co-ordinate is $> 60\ \mu$. *C. deflexum* differs further from *C. macroceros* in that the antapical horns are never ornamented with prominent spines and lists and the girdle is always fully developed.

C. deflexum differs from *C. tenue* O. & S. in that the right horn degree co-ordinate with the 15 μ radius co-ordinate is $< 40°$.

Ventral deflection of antapical horns: The character used by Kofoid to distinguish his new taxon was the "marked" ventral deflection of the antapical horns. As the antapical horns leave the body, they are directed posteriorly and ventrally, so that the recurved distal parts do not lie in the same plane as the body and apical horn. Kofoid found this deflection sometimes in excess of one girdle diameter.

In the Agulhas current NGY specimens it was variable, and sometimes not very marked, when the specimens could have been confused with *C. massiliense var. massiliense* or *C. macroceros* in its cold water form. Indeed, Karsten (1907) included specimens of all three taxa under the name *C. tripos macroceras*. Jörgensen (1911) commented that *C. deflexum* was often confused with *C. macroceros*, but Graham & Bronikowsky (1944) wrote that, once seen, *C. deflexum* was easily recognised.

The ventral deflection of the antapical horns is difficult to measure accurately under the microscope with a graduated fine adjustment screw, because of backlash. It was investigated in 13 NGY specimens, by measuring the difference recorded on the fine adjustment screw when first focussing on the base of the apical horn and then on portions of the antapical horns at the same level, when the specimen was seen in full dorsal or ventral view. Differences recorded varied from 5 to 50 units, and the ventral deflection was roughly the same for left and right horns.

Discussion of some specimens in the literature: C. deflexum was originally described as a subspecies of *C. macroceros*, when '*subsp. macroceros*' was generally regarded as a cold water taxon. There are illustrated records of specimens named *C. macroceros* from South of latitude 30° N., which, from their antapical horn polar co-ordinate measurements, resemble *C. deflexum* rather than *C. macroceros*, but obviously do not have a marked ventral deflection of the antapical horns. They are those of Ostenfeld & Schmidt (1901) from the Red Sea and Gulf of Aden and Klement (1964) from the Gulf of California. They are treated here as specimens of *C. deflexum*.

Peters (1932) investigating the ceratia of the S. Atlantic, incorporated *C. deflexum* in *C. massiliense* because of the presence of many transitional forms, but published no figures or descriptions. Graham & Bronikowsky, after studying the ceratia of the N. Atlantic, concluded that Peters had been dealing with *C. deflexum*-like variants of *C. massiliense*. The specimen they illustrate (l.c. Fig. 22H) is regarded here as belonging to *C. deflexum f. deflectomassum*.

The problem taxon *C. macroceros var. hainanensis* Nie (1936) is now discussed. It was cited by Sournia (1967) as a synonym of '*C. macroceros var. macroceros*'. It was described from Hainan, where individuals were frequently observed from Shin-tsuen. Nie made no comment on any ventral deflection of the antapical horns, describing the thecal walls as less robust than in the type, with a list generally present in the angle between the base of the hypotheca and left horn; the girdle is completely formed, girdle diameter is 64–70 μ and the antapical horns are depicted as smooth. Nie also recorded *C. deflexum*, describing the ventral deflection of the antapical horns as "marked" and giving a girdle diameter of 57–62 μ. The antapical horn polar co-ordinates of Nie's figures of *var. hainanensis* resemble those of figures of some specimens described by Böhm (1931b) as *C. deflexum*. Working on samples from the S.W. Monsoon current, Böhm found *C. deflexum* in stations just to the West and South of Hainan. He observed two forms, one with a diameter of 50–60 μ and short MBC radius co-ordinates, with the left horn MRC occurring before the 75 μ radius co-ordinate, the other with a diameter of 60–68 μ, longer MBC radius co-ordinates and the left horn MRC generally occurring beyond the 75 μ radius co-ordinate. Böhm made no comment on ventral deflection of the antapical horns. In the same area, he found *C. macroceros* to be "rather uncommon as *subsp. gallicum*" in samples from South of 20°N. It is the large forms of *C. deflexum* depicted by Böhm which *var. hainanensis* resembles. The latter is also similar to specimens illustrated by Karsten, (1907, Pl. 51, Fig. 11a, b, classified by Jörgensen (1911) as *C. deflexum*), from an unnamed locality, presumably a station in the East Indies, under the name *C. tripos macroceras*.

C. deflexum is also recorded from the S. China Sea by Steemann Nielsen (1939) and appears to have been illustrated by Okamura (1907) from off the coast of Japan as "*C. macroceras* f.?" for the figure shows what looks like antapical horn deflection (l.c. Fig. 20a).

The East coast of China and Indo China is affected by the warm S.W. monsoon current in summer and the cold N.E. monsoon current in winter, which could cause a variation in the appearance of specimens of *C. macroceros* in the area, but none of the figures of *C. macroceros* from these waters depicted in the literature resembles Nie's figures of *var. hainanensis*. Accordingly, it is treated provisionally as belonging to *C. deflexum*, representing specimens in which the ventral deflection of the antapical horns is not very marked.

General description: Horn disposition and length: Antapical horns slightly to markedly ventrally deflected; initially both horns directed backwards and then recurved anteriorly, usually fairly abruptly; distal parts lie parallel to, to somewhat diverging from, the apical horn, not in the same plane as it or the body; base of left horn makes an indistinct to an obvious angle with base of hypotheca. Antapical horns often found broken (or autotomised?) at level of mid apical horn length, or with closed rounded tips extending to level of two thirds of apical horn length; (Nie, 1936, depicts a specimen in which antapical horns are long, the distal parts slightly undulating, and extend beyond a shortish apical horn). Length of apical horn in NGY specimens: 177–420μ (in one case 60 μ, could have been broken); from literature: 210–425 μ (Jörgensen 1911), 100–450 μ (Nie 1936). *Thecal ornamentation:* Girdle always fully developed; thecal wall generally unmarked, very occasionally thickened with slight ridges; apart from left sulcal list, list usually present in angle between base of left horn and hypotheca, extending along hypotheca base for up to two thirds of length of base; list margin usually smooth, rarely unevenly serrated; occasionally a third narrow list present along base of sulcus; apical horn smooth; antapical horns smooth or, rarely, with minute spines along lower edges in region of recurvature, which may support an insignificant list. (See Figs. 7, 8.)

Distribution: The distribution of *f. deflexum* and *f. deflectomassum* at the NGY Agulhas current stations is shown in Tables 1 and 2.

Sournia (1967) suggested that the records of *C. deflexum* were sparse because of its confusion with *C. macroceros*. Nielsen (1934) desrcibed *C. deflexum* (*sensu stricto*) in the S. Pacific as a typical surface species, from oceanic and neritic waters, rare in truly oceanic waters, and in the Indian Ocean (1939), as very frequent in both neritic and oceanic waters. Graham & Bronikowsky (1944) said it was an intolerant, (closely restricted to regions with surface temperatures of 19°C or more), tropical surface species, with an apparent preference for eutrophic water, for in the Carnegie Pacific samples, the greatest numbers were recorded from stations where the phosphate content was above 25 mg. PO_4/m^3.

F. deflexum appears to be confined to the Pacific and Indian oceans; *f. deflectomassum* is recorded from all oceans and *f. sinensis* has to date only been recorded from the Indian ocean, probably in the vicinity of the East Indies, (the exact locality of Karsten's specimens is uncertain), and the S. China Sea.

Records of any forms of *C. deflexum* from the Mediterranean are not proven. It was not recorded by Jörgensen (1920) and there are only two unillustrated records: Pavillard (1937: 9) listed *C. deflexum* in phytoplankton records for the Monaco Sea, but wrote "identifications doubtful"; Travers & Travers (1962: 57) recorded a single specimen from the Gulf of Marseille, noting "semblait bien caractèrisé et different de *Ceratium macroceros*". Likewise, the presence of *f. deflexum* in the Atlantic is doubtful. Apart from Graham & Bronikowsky's figure of *f. deflectomassum* no other figures of *C. deflexum*-like specimens from the Atlantic have been published.

Ceratium deflexum f. deflexum

C. deflexum (Kofoid) Jörgensen (1911): 64, Pl. 7, Fig. 138; Böhm (1931b): 37, e.p., Fig. 33a–d, *non* e–g, *nec* Fig. 34 (= *f. sinensis*); Steemann Nielsen (1934): 25, Fig. 63; (1939): 14; Nie (1936): 63, Fig. 29 A, B; Schiller (1937): 428, Fig. 467a (= Böhm Fig. 33a), *non* b (= *C. recurvatum* Schröder 1906 Fig. 40); Graham & Bronikowsky (1944): 39, Fig. 22 C, D; Wood (1954): 310, Fig. 237; Sournia (1967): 463, Fig. 86.

"*C. macroceros deflexum* subsp. nov." Kofoid (1907b): 304, Pl. 24, Figs. 13–15.

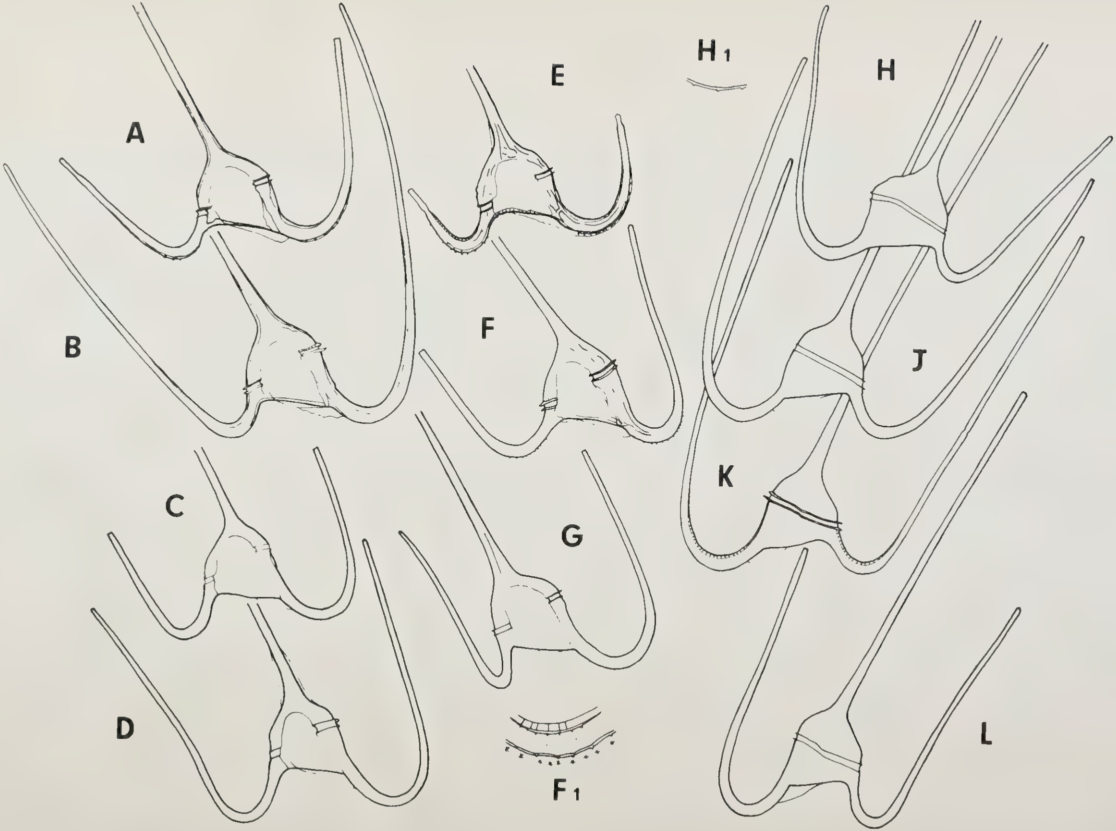


FIG. 7.

C. deflexum (Kof.) Jörg.: All specimens from Agulhas current NGY samples, except **F**; the measurements given for each figure are, in order, the girdle diameter, the sum of left and right horn MRC's and in some cases, the ventral deflection of the antapical horns, (see page 304). **A**, *f. deflectomassum* Rein., 60 μ, 49°, 5 units; **B** – **L**, *f. deflexum*: **B**, specimen from NGY 42, thecal wall in optical section and surface view, 66 μ, 89°, 50 units; **C**, 54 μ, 81°; **D**, 57 μ, 94°, 45 units in left horn, 17 in right; **E**, from NGY 41 (see page 71), thecal wall in optical section and surface view, apparent regeneration of tips of antapical horns, 63 μ, 62°; **F**, from S.W. Indian Ocean station NIOE 121, 66 μ, 63°, 44 units in left horn, 3 in right, specimen seen slightly from one side; **F1**, detail of left horn thecal structure; **G**, 51 μ, 108°, seen slightly from one side; **H**, 63 μ, 80°C, 19 units; **H1**, detail of wall of lower edge of left horn; **J**, 57 μ, 58°, 15 units; **K**, thecal wall in optical section, 60 μ, 52°, 29 units; **L**, 54 μ, 103°.

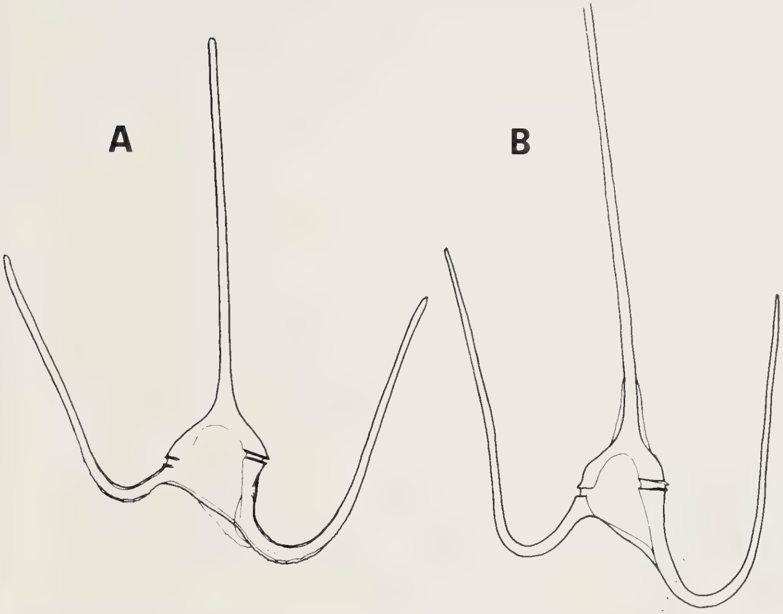


FIG. 8.
C. deflexum (Kof.) Jörg.: Specimens from Agulhas current NGY samples. **A**, *f. deflectomassum* Rein., 60 μ, 49°, 7–10 units; **B**, *f. deflexum*, 57 μ, 94°, 31 units. (See Key to Fig. 7.)

"*C. macroceras* Ehb., f?" Okamura (1907): 128, Pl. 4, Fig. 20a, b *non C. macroceros* (Ehb.) Vanh.

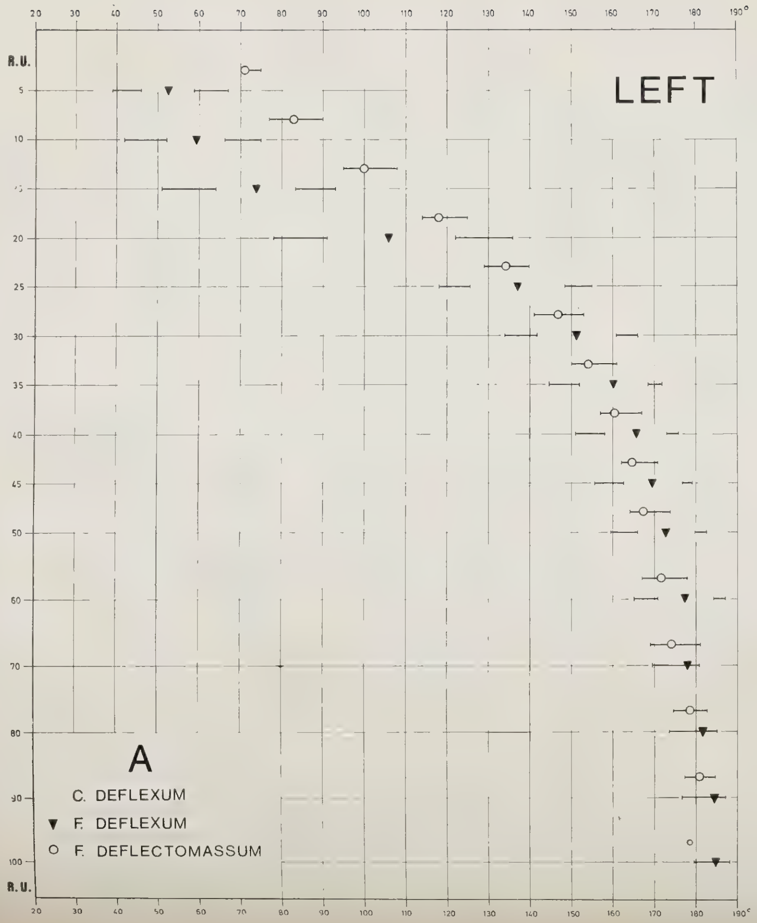
"*C. macroceras* (Ehb.)" Ostenfeld & Schmidt (1901): 167, Fig. 19.

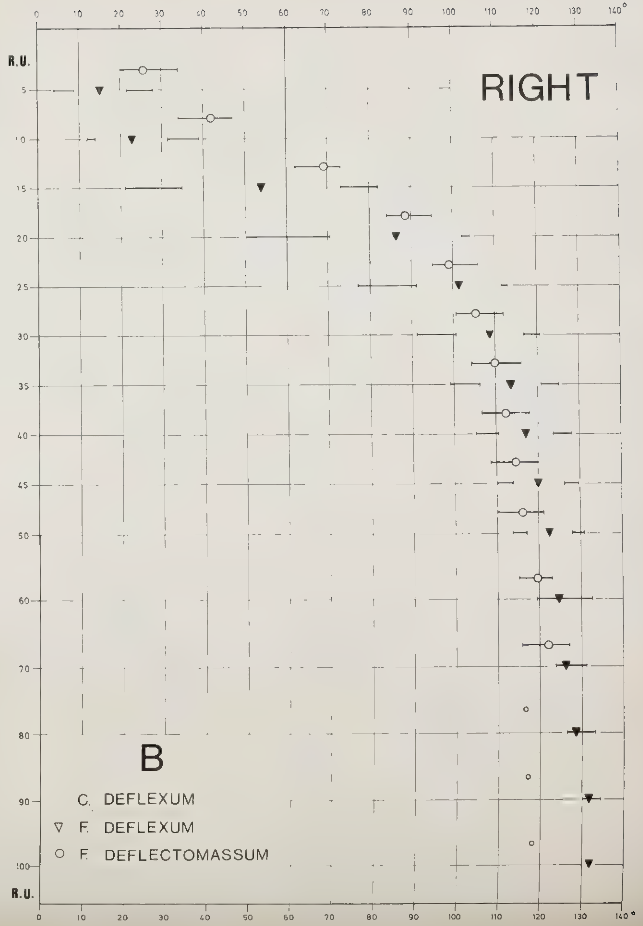
"*C. tripos macroceras*" Karsten (1907) e.p., Pl. 49, Fig. 26a, *non* b (= *f. sinensis*).

"*C. tripos robustum* Ost. & Schm. var." Karsten (1907): 413, e.p., Pl. 51, Fig. 7, *non* Pl. 48, Fig. 13a, b (= *C. vultur* Cl.), *non C. robustum* O. & S. (1901) (= *C. vultur*).

Diagnosis: Differs from *f. deflectomassum* in that the sum of the right and left horn MRC'S is > 50°; differs from *f. sinensis* in that the right horn MBC radius co-ordinate is < 55 μ.

Description: Antapical horns usually markedly ventrally deflected. Horn curvature expressed in polar co-ordinate measurements of two-dimensional camera lucida drawings: *Left horn* MBC co-ordinates 51–78° and 15–48 μ, mostly


LEFT
A
C. DEFLEXUM
▼ F. DEFLEXUM
○ F. DEFLECTOMASSUM
R.U.
5
10
15
20
25
30
35
40
45
50
60
70
80
90
100
R.U.
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190°


RIGHT
B
C. DEFLEXUM
▽ F. DEFLEXUM
○ F. DEFLECTOMASSUM
R.U.
5
10
15
20
25
30
35
40
45
50
60
70
80
90
100
R.U.
0
10
20
30
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50
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100
110
120
130
140°

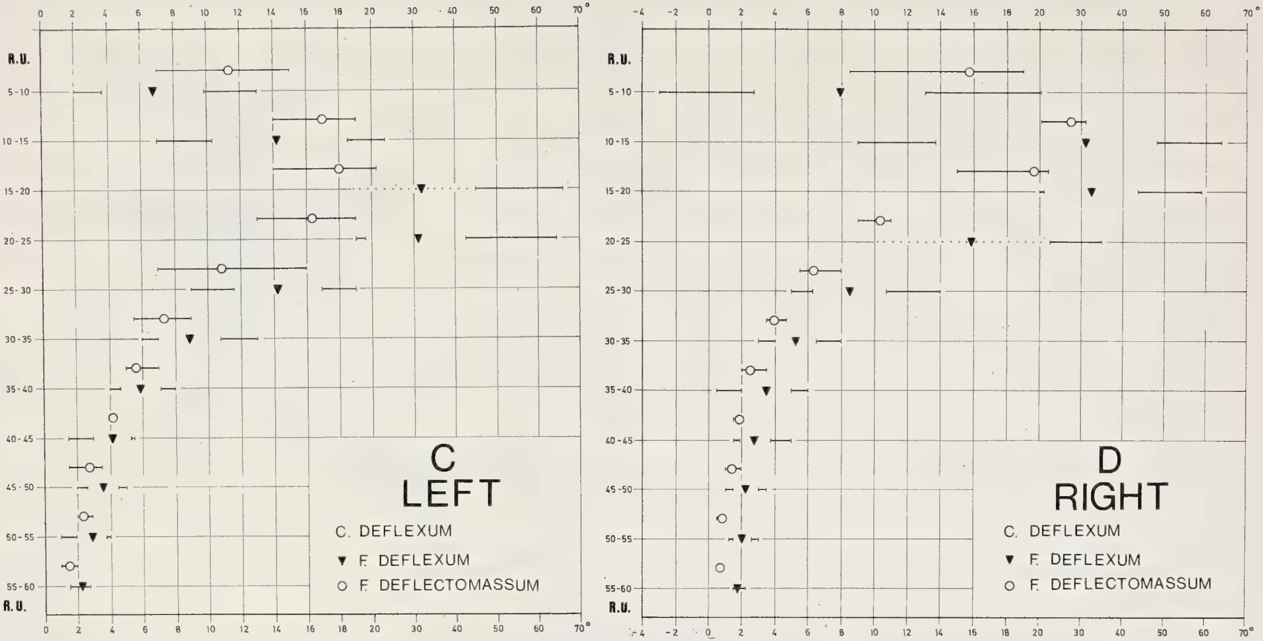


Fig. 9A–D.

C. deflexum (Kof.) Jörg.: Antapical horn curvature in specimens from Agulhas current NGY stations, **A**, curvature of left horn expressed in degrees at 5 R.U. intervals from 5 to 50 R.U. and at intervals of 10 R.U. from 50 to 100 R.U.; **B**, the same for the right horn; **C**, the rate of change of direction of curvature of the left horn expressed in degrees over 5 R.U., from 5–10 to 55–60 R.U.; **D**, the same for the right horn. See Key to Fig. 5.

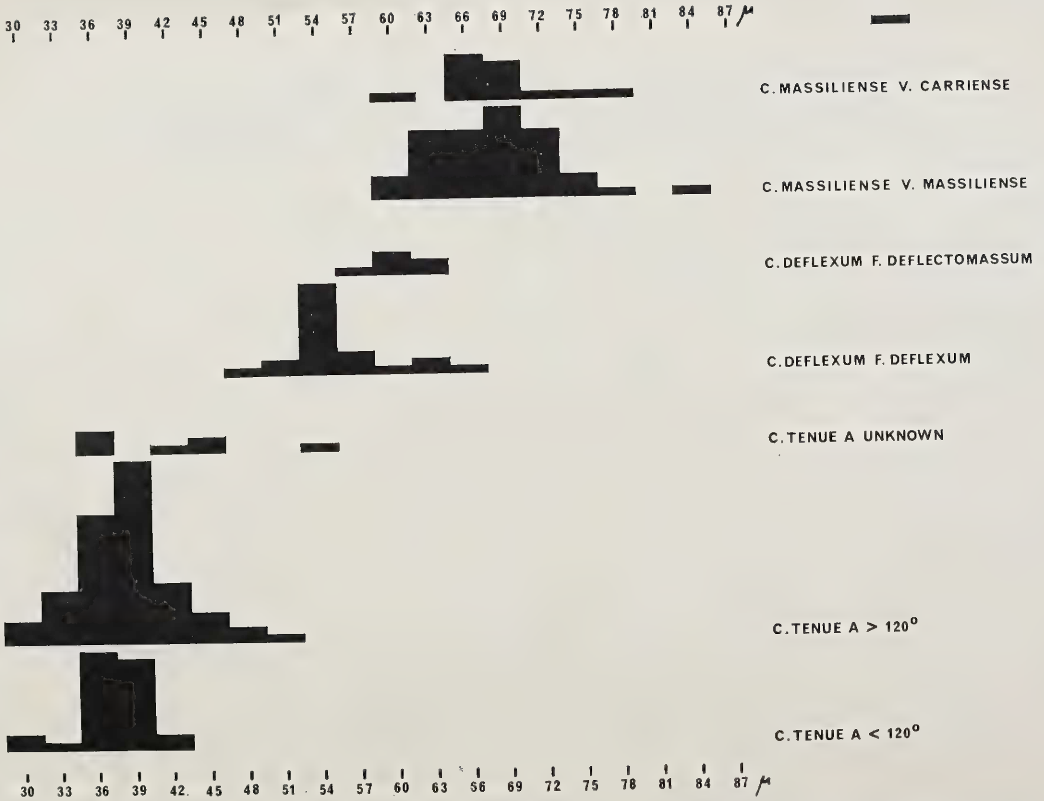


FIG. 10.

Variation in girdle diameter in specimens of *C. massiliense* (Gour.) Kar., *C. deflexum* (Kof.) Jörg. and *C. tenue* O. & S. from NGY Agulhas current samples. (The single bar indicates one specimen; A = right horn degree co-ordinate with 150 μ radius co-ordinate.)

58–68° and 31–40 μ in NGY specimens; degree co-ordinate with 15 μ radius co-ordinate 39–78°, mostly 46–58° in NGY specimens; with 105 μ, 145–179°, (138° in a single case), mostly 152–169° in NGY specimens; with 150 μ, generally exceeding 160°; MRC occurs between 45 and 75 μ radius co-ordinates, very rarely between 30 and 45 μ, and is 21–66°, mostly 26–51° in NGY specimens; $\frac{L90}{D}$ 0,48–1,18, mostly 0,85–1,07 in NGY specimens; $\frac{B}{H}$ 0,42–1,18, mostly 0,66–0,96 in NGY specimens. *Right horn:* MBC degree co-ordinate 26–48°, mostly 32–43° in NGY specimens, less than in left horn by 14–38°, mostly by 20–33° in NGY specimens; MBC radius co-ordinate 25–53 μ, mostly 34–47 μ in NGY specimens, very slightly less than, to up to 20 μ greater than in left horn, 2–7 μ greater than in left horn in most NGY specimens; degree co-ordinate with 15 μ radius co-ordinate 4–28° mostly 8–22°, in NGY specimens, less than in left horn by 18–56°, mostly by 27–48° in NGY specimens; degree co-ordinate with 105 μ radius co-ordinate 93–129°, mostly 106–121° in NGY specimens; MRC generally occurs between 30 and 60 μ radius co-ordinates, very rarely between 15 and 30 μ or 60 and 75 μ, and is 23–64°, mostly 31–55° in NGY specimens; $\frac{R90}{D}$ 0,76–1,91, mostly 0,90–1,30 in NGY specimens. Sum of left and right horn MRC's 51–113°, mostly 64–101° in NGY specimens. (See Fig. 9.)

Dimensions: In NGY specimens: Girdle diameter 48–66 μ, mostly 54–57 μ; length hypotheca 27–42 μ; length epitheca 24–33 μ; angle between base of hypotheca and girdle 23–36°. (See Fig. 10.) *From literature:* Girdle diameter 54–64 μ (Jörgensen 1911), 50–60 μ (Böhm 1931b), 57–62 μ (Nie 1936).

Ceratium deflexum f. sinensis Reinecke forma nova.
C. deflexum: Böhm (1931b): 37, e.p., Figs. 33e–g, 34a, b *non* 33a–d (=*f. deflexum*).
"*C. tripos macroceras*" Karsten (1907) e.p., Pl. 49, Fig. 26a *non* b (=*f. deflexum*), Pl. 51, Fig. 11a, b.
? *C. macroceros var. hainanensis* Nie (1936): 62, Fig. 28A, B.
Diagnosis: Differt a *f. deflexo* et *f. deflectomasso* in eo quod co-ordinatus radii cornus dextri apud locum flexus maximi retrorsum ≥ 60 μ est, et cursus mutationis maximi flexus per 15 μ cornus sinistri plerumque extra co-ordinatum radii 75 μ accidit.

Diagnosis: Differs from *f. deflexum* and *f. deflectomassum* in that the right horn radius co-ordinate at the point of maximum backward curvature is ≥ 60 μ, and the maximum rate of change of direction of curvature over 15 μ generally occurs beyond the 75 μ radius co-ordinate in the left horn.

Description: Ventral deflection of antapical horns sometimes not very marked. Polar co-ordinate measurements of horn curvature in camera lucida drawings from the literature generally as in *f. deflexum*, with the following differences: MBC radius co-ordinates sometimes larger in left horn and always larger in right horn, being 60–78 μ; MBC degree co-ordinate generally smaller in right horn, being 14–33° (40° in one case); difference between left and right horn MBC degree co-ordinates never $< 20°$, being 26–49°; degree co-ordinate with 105 μ radius co-ordinate often lower in both left and right horns; left horn MRC generally occurs beyond 75 μ radius co-ordinate; sum of left and right horn MRC's sometimes as low as 46°; $\frac{L90}{D}$ 0,86–1,57; $\frac{R90}{D}$ 1,63–2,62; $\frac{B}{H}$ 0,90–1,45.

Dimensions: From literature: Girdle diameter 64–70 μ (Nie 1936), 60–68 μ (Böhm 1931b).

Because the evidence for including *var. hainanensis* Nie in *C. deflexum* is circumstantial, the epithet "*hainanensis*" is not retained for this taxon.

C. deflexum f. deflectomassum Reinecke forma nova.
C. massiliense: Graham & Bronikowsky (1944): 38, e.p., Fig. 22H.
C. massiliense f. α macroceroides: Böhm (1931b): 35, e.p., Fig. 32b.
C. macroceros subsp. macroceros: Graham & Bronikowsky (1944): 38, e.p., Fig. 21C.
C. macroceros: Klement (1964): 357, e.p., Pl. 3, Fig. 1.

Diagnosis: Differt a *f. deflexo* in eo quod summa velocitatum maximarum mutationis flexus per 15 μ cornus dextri cornus sinistirque $< 50°$ est; differt a *f. sinense* in eo quod co-ordinatus radii cornus dextri apud locum flexus maximi retrorsum < 55 μ est.

Diagnosis: Differs from *f. deflexum* in that the sum of the maximum rates of change of direction of curvature over 15 μ for left and right horns is $\leq 50°$; differs from *f. sinensis* in that the right horn MBC radius co-ordinate is < 55 μ.

Description: Ventral deflection of antapical horns not very marked. Polar co-ordinate measurements of antapical horn curvature in camera lucida drawings of specimens as in *f. deflexum* save that sum of left and right horn MRC's is 40–50°, right horn MBC degree co-ordinate is never $< 35°$, and right horn degree co-ordinate with 105 μ radius co-ordinate may be as low as 82°. $\frac{L90}{D}$ 0,50–0,88; $\frac{L60}{D}$ 0,73–2,21; $\frac{B}{H}$ 0,30–0,92. (See Fig. 8.)

Dimensions: In NGY specimens: Girdle diameter 57–66 μ; length apical horn up to 350 μ; angle between base of hypotheca and girdle 22–33°. *From literature:* Girdle diameter 66 μ (Klement 1964).

One NGY specimen seen with closed, rounded and slightly swollen antapical horn tips.

This taxon includes specimens which are in some respects intermediate between *C. massiliense var. massiliense* and *C. deflexum sensu stricto*. Steemann Nielsen (1934) noted that forms of *C. massiliense* had a *C. deflexum*-like habit in some of his neritic Pacific samples, and may have been referring to the present taxon.

TAXON INCERTAE SEDIS

C. recurvatum Schröder (1906): 367, Fig. 40.

C. deflexum f. recurvatum (Schr.) Jörgensen (1911): 65, 123, Pl. 7, Fig. 138 (= Schröder Fig. 40).

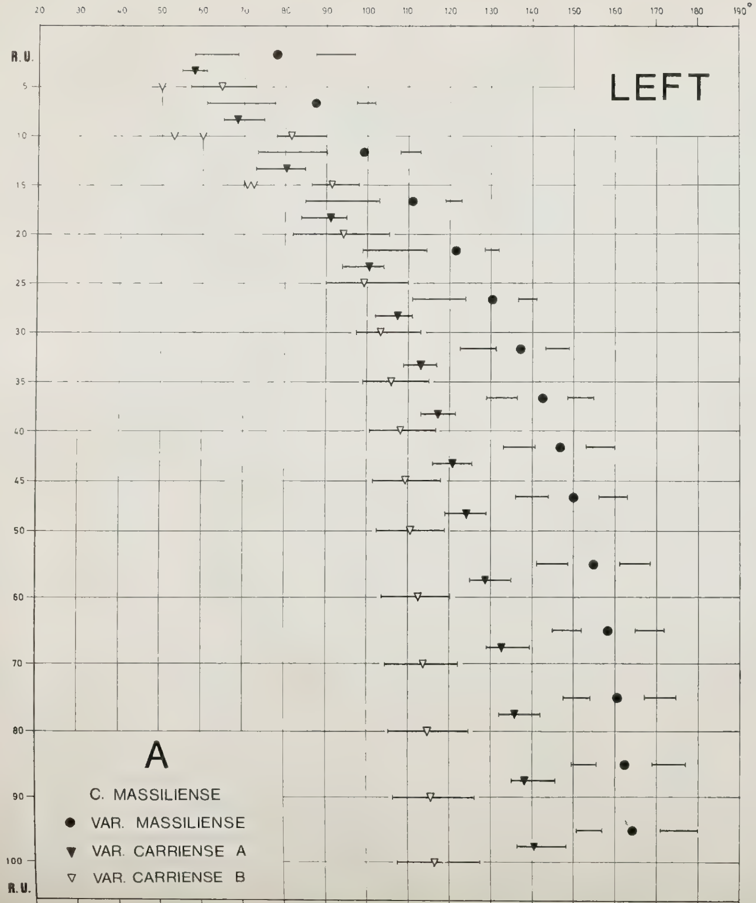
C. deflexum: Schiller (1937): 428, p.p., Fig. 467b (Schröder Fig. 40), *non* a (= *C. deflexum f. deflexum*).

This problematic form was found in the Arabian Sea by Schröder and later a second specimen was seen in Schröder's sample by Jörgensen (1911) who lost it before he could draw or measure it. From the scale, the diameter of Schröder's specimen is about 56 μ. If it is a freak, then it does not have taxonomic status, but, whether a freak or not, the question arises: is it related to *C. deflexum*? The shape of the body in Schröder's figure indicates that it was probably drawn seen in full ventral aspect. Polar co-ordinate measurements of the curvature of the right horn show an MRC of about 10°, which is lower than recorded in any camera lucida drawings of *C. deflexum*, while the MBC radius co-ordinate is about 75 μ.

Ceratium massiliense (Gourret) Karsten (1906): 145.

Diagnosis: In the specimens examined, *C. massiliense var. massiliense* and most specimens of *C. massiliense var. carriense* (Gour.) Rein. differ from *C. macroceros* (Ehb.) Vanh. in that the ratio $\frac{B}{H}$ is $< 0,90$; (*C. massiliense* differs from the single specimen of *C. macroceros* recorded in the Agulhas current in which this ratio was 0,83, in that the girdle diameter is ≥ 60 μ); the few specimens of *var. carriense* in which the ratio $\frac{B}{H}$ is $\geq 0,90$, but always $< 1,50$, differ from *C. macroceros* in that the right horn MRC is $\leq 10°$ and the sum of left and right horn MRC's is $\leq 25°$; (specimens of *var. carriense* in which the ratio $\frac{B}{H}$ is $\geq 0,90$, differ from the three specimens of *C. macroceros* recorded in which the right horn MRC was $\leq 10°$, in that the ratio $\frac{B}{H}$ is $< 1,50$ *and* the sum of left and right horn MRC's is $\leq 25°$ *and* the girdle diameter is ≥ 60 μ); specimens of *var. carriense* in which the ratio $\frac{B}{H}$ is $\geq 1,10$, differ further from *C. macroceros* in that the difference between the left horn radius co-ordinates of the tangent, parallel to the girdle, to the lower edge of the antapical horn and of the point of MBC, is > 100 μ.

C. massiliense differs from *C. deflexum* (Kof.) Jörg. in lacking a marked ventral deflection of the antapical horns; expressed in terms of polar co-ordinate


20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190°
R.U.
5
10
15
20
25
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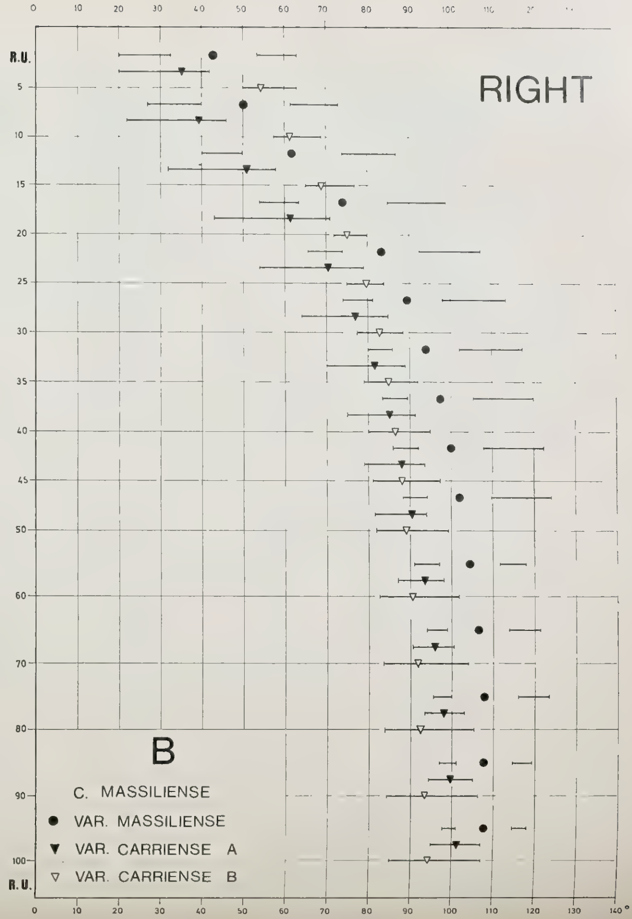
40
45
50
60
70
80
90
100
R.U.
LEFT
A
C. MASSILIENSE
● VAR. MASSILIENSE
▼ VAR. CARRIENSE A
▽ VAR. CARRIENSE B


0 10 20 30 40 50 60 70 80 90 100 110 120 130 140°
R.U.
5
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RIGHT
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C. MASSILIENSE
● VAR. MASSILIENSE
▼ VAR. CARRIENSE A
▽ VAR. CARRIENSE B

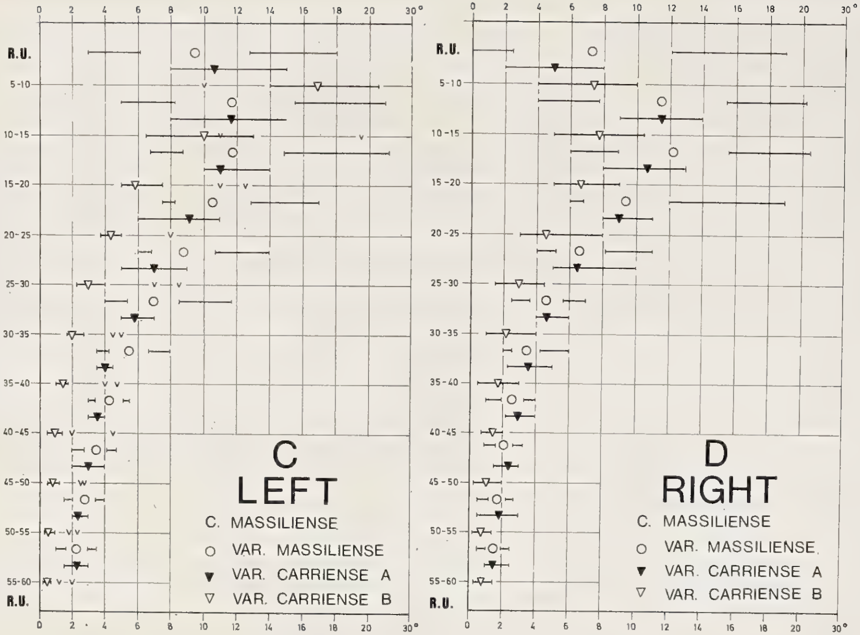


FIG. 11A–D.

C. massiliense (Gour.) Karst.: Antapical horn curvature in specimens from Agulhas current NGY stations. **A**, curvature of left horn expressed in degrees at 5 R.U. intervals from 5 to 50 R.U. and at 10 R.U. intervals from 50 to 100 R.U.; **B**, the same for the right horn; **C**, the rate of change of direction of curvature of the left horn expressed in degrees over 5 R.U. from 5–10 to 55–60 R.U.; **D**, the same for the right horn. In *var. carriense* A, the left horn degree co-ordinate with the 100 R.U. radius co-ordinate is > 130°, in *var. carriense* B, this co-ordinate is < 130°. See Key to Fig. 5.

measurements of two-dimensional camera lucida drawings, *C. massiliense* differs from *C. deflexum* in that the sum of the left and right horn MRC's is $< 40°$; (a single specimen of *var. carriense*, (Jörgensen 1911, Fig. 150a), in which the sum of left and right horn MRC's was $> 40°$, differed from *C. deflexum f. deflexum* and *C. deflexum f. deflectomassum* Rein. in that the left horn degree co-ordinates with the 105 and 150 μ radius co-ordinates were $< 130°$, and from *C. deflexum f. sinensis* Rein. in that the right horn MBC radius co-ordinate was $< 60\ \mu$).

C. massiliense differs from *C. trichoceros* (Ehb.) Kof. in that the left horn MRC occurs before the 75 μ radius co-ordinate; (the single specimens recorded of *var. massiliense* (from the Agulhas current) and of *var. carriense* (Karsten 1907, Pl. 49, fig. 27e) in which the left horn MRC occurred beyond the 75 μ radius co-ordinate, differed respectively from *C. trichoceros*, in that, in the first, the left horn degree co-ordinate with the 15 μ radius co-ordinate was $> 90°$, and in the second, the girdle diameter was $> 60\ \mu$ and the left horn MBC degree co-ordinate $< 70°$).

C. massiliense differs from *C. tenue* O. & S. in that the girdle diameter is $\geq 60\ \mu$.

Taxonomic history and present treatment of taxa: C. massiliense, one of the most variable species of the genus, was originally described as *C. tripos var. massiliense* by Gourret (1883: 27, Pl. 1, Figs. 2, 2a), together with *C. carriense* (l.c.: 38, Pl. 4, Fig. 57). From his drawings, it is evident that Gourret confused dorsal and ventral views and considered the apical horn to lie posteriorly. In none of the figures mentioned are lists or spines depicted. Gourret considered that the essential difference between the two taxa was that in *C. carriense*, the girdle was "concave en bas". It would appear that the specimen in Fig. 57 is drawn tilted so that the base of the hypotheca is nearest the viewer, which would account for the appearance of the girdle as "angled" in mid diameter towards the apical horn. The specimen in Fig. 2a is drawn seen slightly from one side.

In 1900, Cleve described a species, "*C.* (*tripos var.*?) *volans*": "characterised by the straight and very long posterior horns, which proceed in a right angle to the apical horn . . . it may be possible that it is the same as *C. carriense* Gourret, which I dare not decide, without comparing the original specimens." (1900a: 15, Pl. 7, Fig. 4).

Unfortunately, in both Cleve's Fig. 4 and Gourret's Fig. 57, only the proximal parts of the antapical horns are shown, making them, together with Gourret's Fig. 2a, very unsatisfactory iconotypes. (See Fig. 16 F, G.)

The correct citation of the combination *Ceratium massiliense* has been a matter of dispute. The combination was first used by Karsten thus: "Die weiter folgenden Formen . . . gleichen am meisten dem *Ceratium massiliense* Gourret (l.c. S. 27, Taf. 1, Fig. 2, 2a), ohne jedoch mit ihm identifiziert werden zu können." The forms he referred to were "*C. tripos protuberans* n. sp." and "*C. tripos macroceroides* n. sp.", both placed by Jörgensen (1911) in the species he then cited as "*C. massiliense* (Gourret)". Pavillard (1907) was the first to cite the species as *C. massiliense* (Gourret) Karsten applying this to Gourret's Fig. 2a, while he considered Fig. 2 to belong to "*C. aequatoriale*" Schröder. Jörgensen (1920), who in 1911 had considered Gourret's Fig. 2 as belonging to *C. massiliense* and his Fig. 2a as belonging to *C. carriense* Gourret, proposed the illegal combination "*C. massiliense* (Gourret, Karsten) Jörg.". Sournia (1967), who followed Jörgensen's treatment of Gourret's figures, considered the citation *C. massiliense* (Gour.) Kars. to be invalid, invoking Articles 33 and 34 of the International Code, and cited the combination as "*C. massiliense* (Gour.) Jörg.". But, as it is printed in the "Atlantische Phytoplankton", the combination *C. massiliense* (Gourret) Karsten is validly published. The combination is clearly indicated, with a full reference to the original author, and cannot be considered as an incidental mention. Karsten's species concepts regarding *Ceratium* were often confused, and his wording definitely shows that he considered his two new species and that of Gourret as three separate taxa.

Significant steps in the taxonomic history of this complex up to 1911 are shown in Table 3. Sournia (1966, 1967) recognised the following taxa: *C. massiliense var. massiliense*, *C. massiliense var. protuberans* (Kars') Jörg., *C. massiliense f. armatum* (Kars.) Jörg., *C. carriense var. carriense* Gour. and *C. carriense var. volans* (Cl.) Jörg.

No workers have combined *C. massiliense* and *C. carriense*, although many have commented on their great variability and Jörgensen himself (1911) noted that they were confusingly similar. Graham & Bronikowksy (1944) suggested that the two species might be identical, and Wood (1954) observed that there seemed more reason to treat the components of "*C. horridum* (Cl.) Gran" (*C. tenue* O. & S.) as separate species than to divide *C. carriense* from *C. massiliense*. Steemann Nielsen (1939) referred to the *Formenkries≫ massiliense* «, which included *C. massiliense*, *C. carriense* and *C. deflexum*. Earlier (1934) he had noted specimens of *C. massiliense* in neritic waters which resembled *C. carriense var. carriense* in habit.

An examination of NGY Agulhas current specimens and those depicted in the literature leads to the conclusion that *C. massiliense* and *C. carriense* should indeed be treated as a single species.

The differences between '*C. carriense*' and *C. massiliense* as given by Jörgensen (1911) are as follows: in '*C. carriense*', the antapical horns are far more spreading; the right horn is more divergent, the proximal part making an obtuse angle with the distal part, while in *C. massiliense* this is more of a right angle; the base of the hypotheca is more depressed between the bases of the antapical

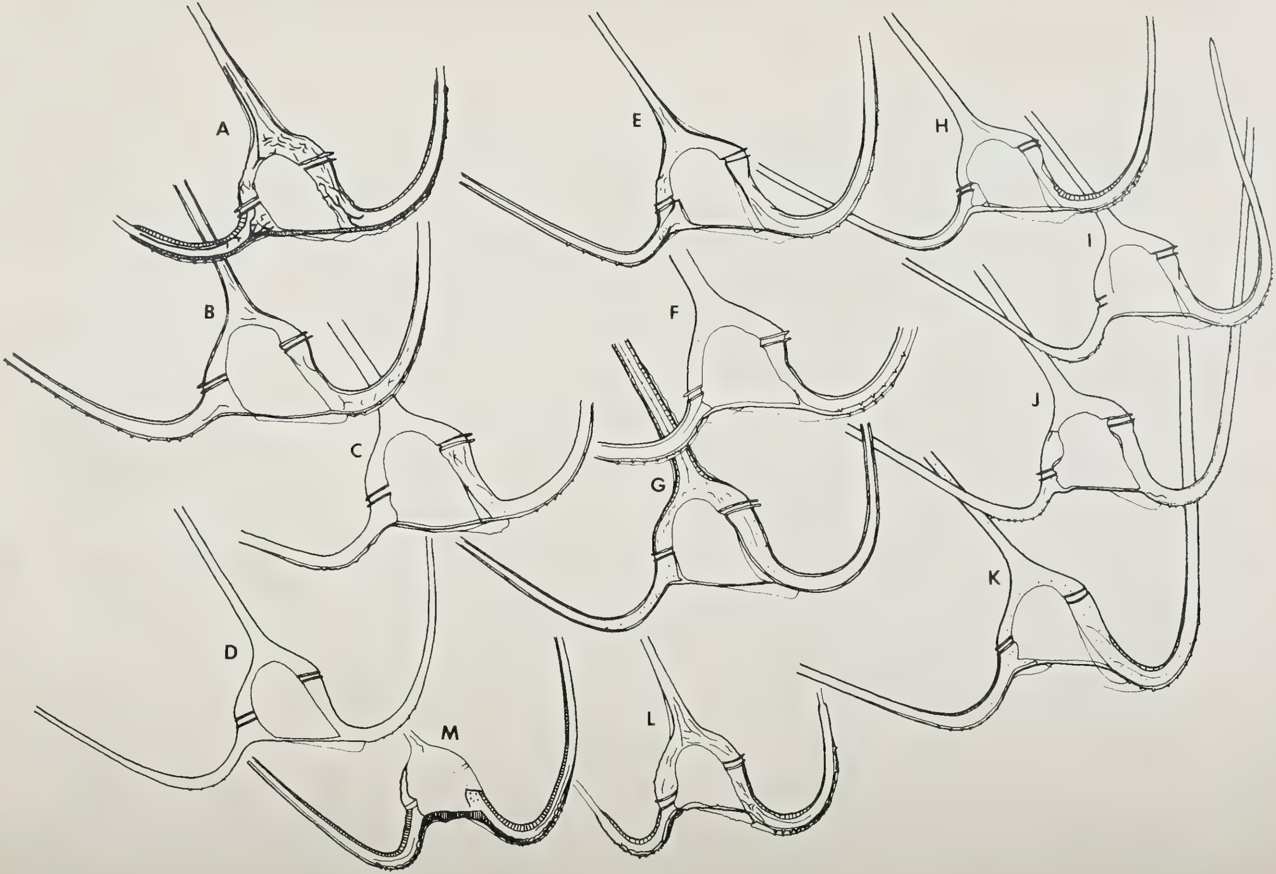


FIG. 12.

(Measurements for each specimen given in the following order: girdle diameter, left horn degree co-ordinate with 15 μ radius co-ordinate, and, in **I–L**, sum of left and right horn MRC's.) **A–H**, **J**, **K**, *C. massiliense var. massiliense* (Gour.) Kars.: **A** 69 μ, 90°; **B** 69 μ, 90°; **C** 72 μ, 96°; **D** 60 μ, 85°; **E** 63 μ, 72°; **F** 75 μ, 77°; **G** 69 μ, 68°; **H** 63 μ, 88°; **J** 66 μ, 65°, 38°; **K** 69 μ, 58°, 38°; **I**, *C. deflexum f. deflectomassum* Rein.: 60 μ, 70°, 49°; **L**, *C. deflexum f. deflexum* (Kof.) Jörg.: 63 μ, 55°, 62°; **M**, *C. macroceros* (Ehb.) Vanh.: 51 μ, 45°. All specimens from Agulhas current NGY samples, thecal wall shown in optical section and surface view.

horns; the base of the left horn is "less straight", (*gerade*—Jörgensen's meaning is not clear), and makes a definite angle with the base of the hypotheca, which angle is generally smaller than the indistinct angle in *C. massiliense;* the left profile of the hypotheca is straight or weakly convex, while in *C. massiliense* it is somewhat concave and generally oblique; the angle made by projections of the girdle and the base of the hypotheca is smaller, as is the perpendicular distance *B*.

Polar co-ordinate measurements of antapical horn curvature in NGY specimens showed slight discontinuities only in the co-ordinates of the left horn, which delimited three groups; in the first, approximating Jörgensen's concept of *C. massiliense*, the left horn degree co-ordinate with the 150 μ radius co-ordinate was $> 130°$; in the second and third groups, approximating Jörgensen's concept of '*C. carriense*', the left horn was more spreading and the degree co-ordinate with the 150 μ radius co-ordinate was $< 130°$; in the second group, the degree co-ordinate with the 300 μ radius co-ordinate was $> 130°$ and in the third group it was $< 130°$. (See Fig. 11A). While there were no discontinuities in the right horn polar co-ordinates, this horn tended to be more spreading in groups two and three, (see Fig. 11B). Specimens of the first group were found in which the angular delimitation of the base of the hypotheca by the bases of the antapical horns was very marked, (in two such instances, the left horn degree co-ordinates with the 150 μ radius co-ordinates were 143° and 159°), as is the case in a figure of Karsten's (1906 Pl. 22, Fig. 29a) cited by Jörgensen in the synonomy of *C. massiliense!* The left horn degree co-ordinate with the 15 μ radius co-ordinate was 58–97°, mostly 70–90° in group one, and 50–73° in groups two and three, while the left horn MBC degree co-ordinate was 63–90° in group one, mostly 72–86°, and 53–73° in groups two and three. The left profile of the hypotheca was generally sloping and slightly concave in group one, but this condition was found in some specimens of groups two and three, and straight or slightly convex left profiles, common in groups two and three, were also found in group one. The angle between the base of the hypotheca and the girdle was 22–34°, mostly 25–31° in group one and 19–31° in groups two and three. The ratio $\frac{B}{H}$ was 0,14–0,81, mostly 0,22–0,50 in group one, and 0,30–0,90 in groups two and three.

No discontinuities were shown between these groups in measurements of other characters such as girdle diameter, MBC radius co-ordinates, MRC and position of MRC, and the ratios $\frac{L90}{D}$ and $\frac{R90}{D}$

Measurements of polar co-ordinates of specimens from the literature support these observations, but eliminate the discontinuity between groups two and three, (see Table 4). It is of interest to note that the specimen of unknown size depicted by Pavillard (1905, Pl. 1, Fig. 1) as '*C. volans*' and cited under '*C. carriense*' by Jörgensen (1911), at a diameter of 69 μ, has a value for the left horn degree co-ordinate with the 105 μ radius co-ordinate of approximately 135°, which places it in group one.

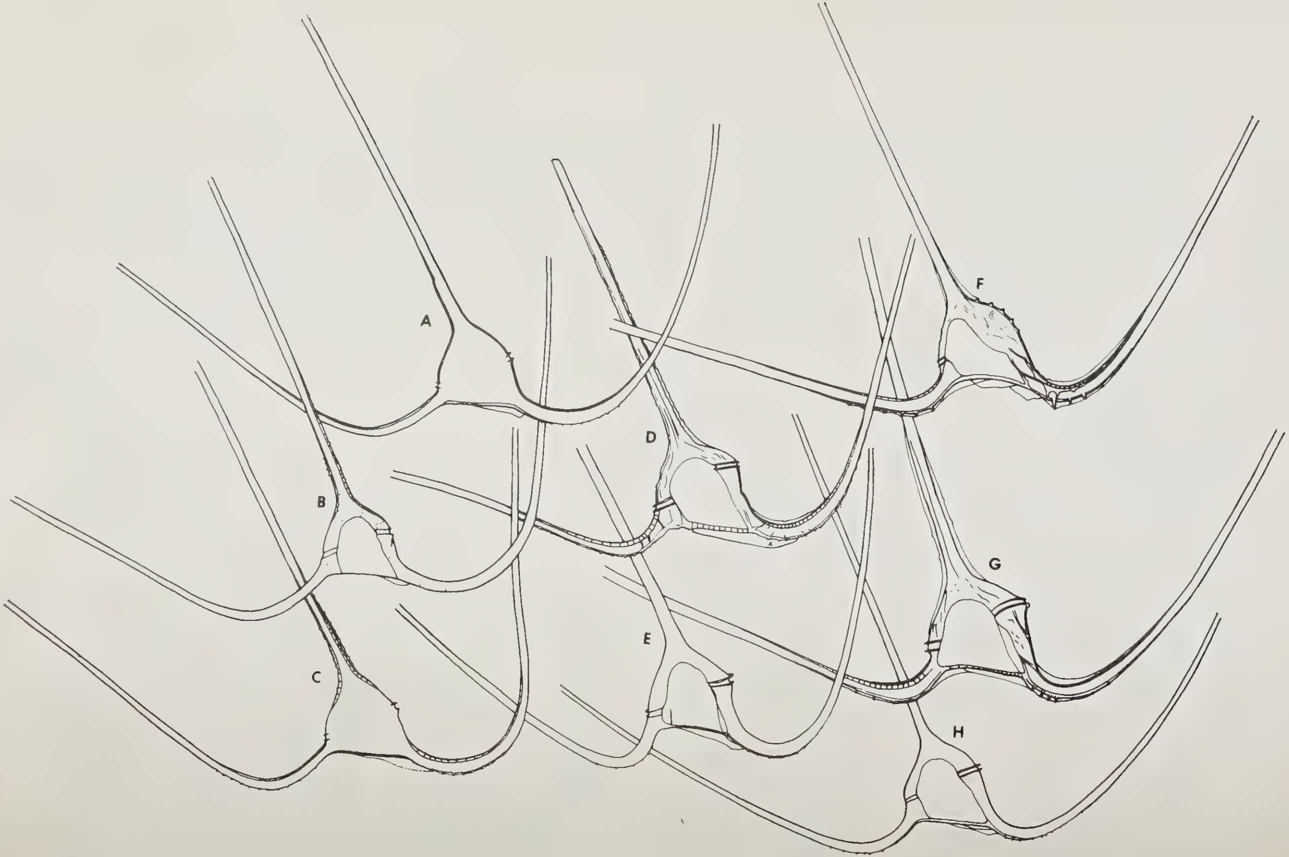


FIG. 13.

(Measurements for each specimen given in this order: girdle diameter, where left horn MRC occurs, and left horn degree co-ordinates with 15 μ, 150 μ and 300 μ radius co-ordinates.) **A**–**C**, *C. trichoceros var. contrarium* (Gour.) Schill.: specimens with diverging antapical horns, included here to show difference in antapical horn curvature; **A** 57 μ, 75–105 μ, 64°, 123°, 150°; **B** 57 μ, 105–120 μ, 70°, 133°, 160°; **C** 57 μ, 90–120 μ, 65°, 144°, 166°; **D** and **E** *C. massiliense var. massiliense* (Gour.) Karst.: **D** 69 μ, 45–75 μ, 77°, 141°, 156°; **E** 63 μ, 60–75 μ, 60°, 140°, > 150°; **F–H**, *C. massiliense var. carriense* (Gour.) Rein.: **F** 72 μ, 30–45 μ, 60°, 129°, 142°; **G** 75 μ, 45–60 μ, 56°, 119°, 137°; **H** 66 μ, 15–45 μ, 61°, 123°, ≃ 140°. All specimens from Agulhas current NGY samples, thecal wall shown in surface view and optical section, horns incompletely shown

Thus, when the characters, which according to Jörgensen distinguish *C. massiliense* from '*C. carriense*', are actually measured, differences between the two are shown to be far less than warrants their recognition as two separate species, and they are accordingly treated as varieties of a single species.

Ceratium massiliense var. massiliense
(See Figs. 12A–H, J, K, 13D, E, 14A, B and 15.)
Sournia (1966): 1982; (1967): 466; Paredes (1969/70): 44, Pl. 22, Fig. 153.
C. massiliense (Gourret) Karsten (1906): 145.
Pavillard (1907): 226; (1916): 17; (1931): 88; Jörgensen (1911): 66, Pl. 7, Figs. 140–142; (1920): 85, Fig. 78; Schröder (1911): 646; Mangin (1912): 24, Fig. 7; Forti (1922): 66, Pl. 3, Fig. 51 (= Jörgensen Fig. 141); Dangeard (1927): 378; Abé (1927): 430, Fig. 48A, B; Paulsen (1930): 89, Fig. 55C–F, *non* A, B (= *C. trichoceros var. contrarium* (Gour.) Sch.); Böhm (1931a): 383; Peters (1932): 50, Pl. 1, Fig. 2a, b, Pl. 2, Fig. 10f, Pl. 3, Fig. 13a; Wang & Nie (1932): 301, Fig. 14; Steemann Nielsen (1934): 25, Figs. 60–62; (1939): 14; Nie (1936): 65; Graham & Bronikowsky (1944): 38, Fig. 22E–G, J, K; Silva (1949): 361, Pl. 7, Fig. 3; Margalef & Duran (1953): 42, Fig. 12m–p, ?q, r (figures of an abnormal form of uncertain affinity); Gaarder (1954): 14; Margalef (1957): 48, Fig. 3g; Halim (1960): 180, Pl. 5, Fig. 15; Klement (1964): 357, Pl. 3, Fig. 2; López (1966): 333, Figs. 50, 51; Taylor (1967): 463, Pl. 91, Fig. 39, "intermediate form"; Steidinger & Williams (1970): 46, Fig. 30a–e.
C. tripos var. massiliense Gourret (1883): 27, Pl. 1, Fig. 2, *non* 2a (= *var. carriense* (Gour.) Rein.); Daday (1888): 99.
C. tripos var. macroceras f. massiliensis (Gour.) Schröder (1900): 15.
C. massiliense α macroceroides (Kars.) Jörgensen (1920): 86, (used instead of var. or *f. massiliense*).
C. massiliense f. α macroceroides: Böhm (1931a): 362; (1931b): 35, Fig. 32a, c, d *non* b (= *C. deflexum f. deflectomassum* Rein.).
C. massiliense f. macroceroides: Schiller (1937): 424, Fig. 436a; Rampi (1939): 308, Fig. 33; Wood (1954): 308, Fig. 235a; Klement (1964): 357; Halim (1963): 498, Fig. 28.
C. massiliense var. macroceroides: Taylor (1967): 463.
C. tripos macroceroides Karsten (1906)*: 145, Pl. 22, Fig. 28a, b.
C. massiliense var. protuberans (Kars.) Jörgensen (1911): 67, Pl. 7, Fig. 143, Pl. 8, Figs. 144, 145; (1920): 86, Fig. 79; Schröder (1911): 646; Pavillard (1916): 17; Forti (1922): 67, Pl. 4, Fig. 53; Dangeard (1927): 378, Fig. 43b; Graham & Bronikowsky (1944): 38, Fig. 22I; Silva (1949): 361; Sournia (1966): 1982; (1967): 467; Paredes (1969/70): 44, Pl. 22, Fig. 154.
C. massiliense f. protuberans (Kars.) Böhm (1931a): 362, Fig. 16; (1931b): 35; Schiller (1937): 424, Fig. 463c, d (= Jörgensen Fig. 144); Rampi (1939): 310,

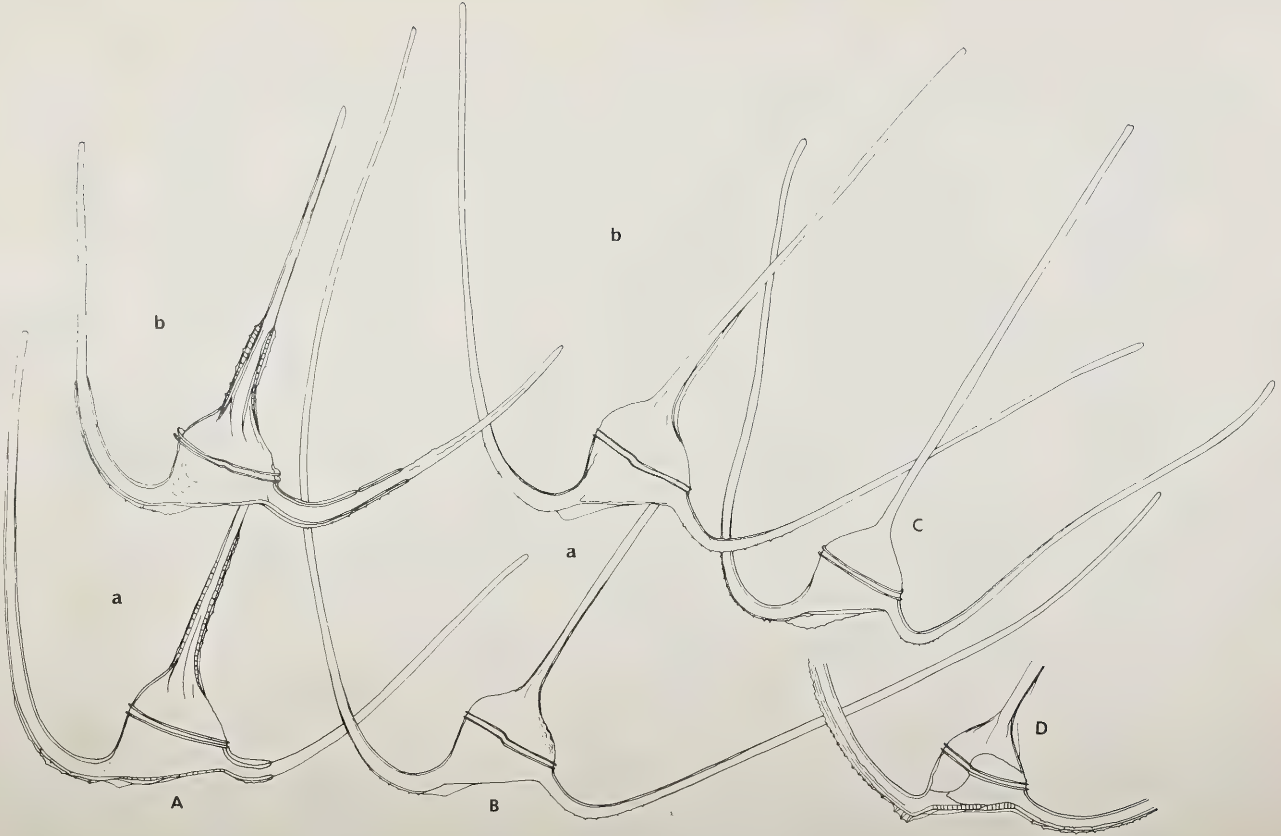


Fig. 14.

(Measurements given for each specimen given in following order: girdle diameter, left horn degree co-ordinate with 15 μ radius co-ordinate and sum of left and right horn MRC's.) **A** and **B**, *C. massiliense var. massiliense* (Gour.) Karst.: two celled chains, with regeneration of apical and antapical horns in **A**, (after autotomy?), **Aa** 66 μ, 89°, 24°; **Ab** 66 μ, 84°, 23°; **Ba** 63 μ, 70°, 27°; **Bb** 66 μ, 70°, 30°; **C**, *C. deflexum f. deflectomassum* Rein.: 63 μ, 70°, 47°; **D**, *C. vultur f. sumatranum* (Karst.) Sournia: long apical horned specimen, included to show distinctive base of left horn, 66 μ. All specimens from Agulhas current NGY samples, thecal wall shown in optical section and surface view.

Fig. 40; Wood (1954): 308, Fig. 235c; Gaarder (1954): 14; Halim (1960): 180; (1963): 499, Fig. 29.

C. protuberans (Kars.) Paulsen (1930): 89, Fig. 56A–C.

C. tripos protuberans Karsten (1906): 145, Pl. 22, Fig. 27a–g.

C. massiliense f. crassum sensu Jörgensen (1920): 87.

C. tripos macroceras var. crassa Karsten (1907): 411, e.p., Pl. 49, Fig. 27a, *non* c, e, (c = *C. macroceros*, e = *var. carriense*).

C. tripos flagelliferum var. crassa Karsten (1907): 410, Pl. 49, Fig. 25a–c.

C. massiliense f. armatum sensu Jörgensen (1911): 67, e.p., Pl. 8, Fig. 146; Forti (1922): 67, Pl. 4, Fig. 52 (= Jörgensen Fig. 146); Schiller (1937): 424, Fig. 463b (= Jörgensen Fig. 146); Rampi (1939): 310, Fig. 32; Wood (1954): 308, Fig. 235b; Sournia (1967): 468, Fig. 87 (= Peters (1932) Pl. 3, Fig. 16a), Fig. 88 (= Rampi Fig. 32).

C. massiliense var. armatum sensu Peters (1932): 50, Pl. 3, Fig. 16a; Graham & Bronikowsky (1944): 38, Fig. 22L.

Non C. tripos var. macroceras f. armata Karsten (1905): 132, Pl. 19, Figs. 7, 8; (1906): 146, (? = *C. massiliense f. armatum* (Kars.) Jörg. 1920).

C. massiliense f. ellipticum Böhm (1931a): 362, e.p., Fig. 17a, *non* b, *non* 18a, b (= *var. carriense*).

C. volans sensu Pavillard (1905): 54, e.p., (includes *var. carriense*), Pl. 1, Fig. 1; Okamura (1907)*: 130, e.p., Pl. 4, Fig. 18c, d, e *non* 18a, b (18a = *C. tenue*, 18b = *var. carriense*).

"*C. volans* forma": Schröder (1906)*: 363, Fig. 34.

C. tripos volans var. campanulata Karsten (1907): 408.

C. *aequatoriale* Schröder (1906): 360, Fig. 32; Pavillard (1907): 226.

C. tripos intermedium var. aequatorialis (Schr.) Karsten (1907): 412, Pl. 49, Fig. 21a, b.

C. ostenfeldii Kofoid (1907b): 305, e.p., Pl. 26, Figs. 22, 23 *non* 24, 25, (24 *C. macroceros*, 25 = *var. carriense*).

C. tripos intermedium var. hundhausenii sensu Karsten (1907): 413, Pl. 50, Fig. 10, *non C. hundhausenii* Schröder (= *var. carriense*).

C. horridum f. intermedia (Jörg.) Ost.: Okamura (1907): 129, e.p., Pl. 4, Figs. 21a, c *non* b, *non* Fig. 23 (21b = *C. tenue*, 23 = abnormal form of uncertain affinity, probably = *C. macroceros*).

C. horridum f. laevis Okamura (1907)*: 129, e.p., Pl. 4, Fig. 21d, f, h *non* e,g *e* = *C. tenue*, g = *C. contortum* (Gour.) Cl.).

C. horridum subsp. buceros var. molle sensu Margalef & Duran (1953): 42, Fig. 12j, k.

C. pavillardii sensu Dangeard (1927): 378, Fig. 42a, *non C. pavillardii* Jörgensen (= *C. vulture var. pavillardii* (Jörg.) G. & B.).

C. vultur f. regulare Graham & Bronikowsky (1944): 41, Fig. 23C.

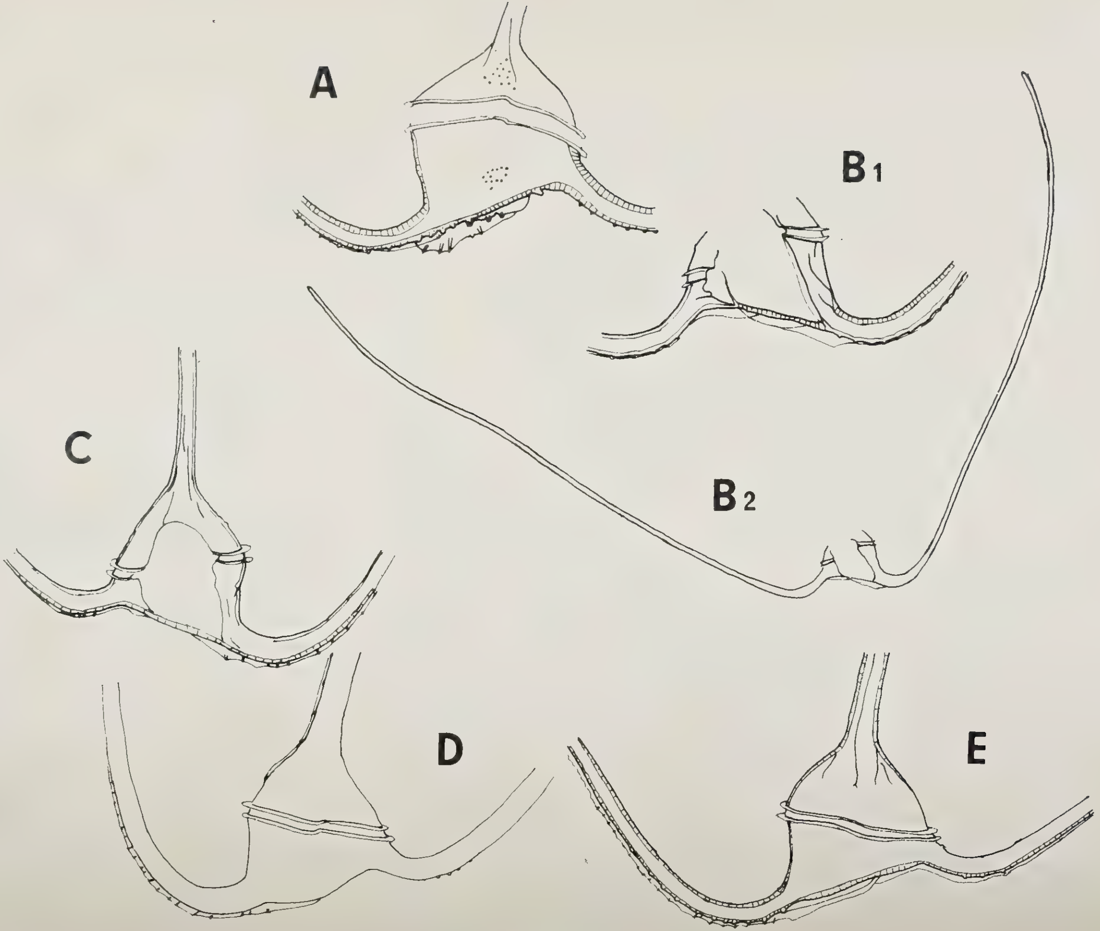


FIG 15

C. massiliense var. massiliense (Gour.) Kars.: Showing further variations in antapical spines and lists. Girdle diameter: **A** 84 μ, specimen broken, **B** 72 μ, shown at two magnifications, **C** 69 μ, **D** 69 μ, **E** 75 μ. Thecal wall shown in optical section and surface view in all save **D**, all specimens from Agulhas current NGY samples.

C. contrarium (Gour.) Pav.: Graham & Bronikowsky (1944) e.p., Fig. 22E, *non* Fig. 24A, B (= *C. trichoceros var. contrarium* (Gour.) Sch.).
C. tripos longipes sensu Karsten (1907): 412, Pl. 48, Fig. 11 a, b, Pl. 51, Figs. 12, 13.
C. tripos longipes f. ventricosa Karsten (1906): 145, Pl. 21, Figs. 26, 26a.
C. tripos longipes var. cristata Karsten (1907): 413, e.p., Pl. 48, Fig. 12c, ? *non* a, b (? = *f. armatum*).
"*Ceratium* sp." Chun (1903): 64, Fig. b.
C. tripos macroceros sensu Entz (1902) e.p., Pl. 2, Figs. 17, 18, Pl. 6, Figs. 40, 41; sensu Karsten (1906): 145, e.p., Pl. 22, Fig. 29a, *non* b–d (= *C. macroceros*); (1907): 411, e.p., Pl. 49, Fig. 27a, *non* b–e (b, c, = *C. macroceros*, d, e = *var. carriense*).
? *C. tripos var. macroceros:* Stein (1883) Pl. 16, Fig. 9 (Antapical horns are shown with closed pointed tips, extending to level of about one third of length of apical horn, but left antapical horn definitely curved backwards initially.)
? *C. macroceros:* Wood (1954) e.p., Fig. 238a.
? *C. tripos var. macroceras f. undulata* Schröder (1900)*: 16, Pl. 1, Fig. 17k, *non* l, m (l = *C. tenue*, m = *C. vultur var. pavillardii*—Jörgensen (1920) cited Fig. 17m in the synonomy of both '*C. pavillardii*' and *C. massiliense*).
? *C. tripos var. macroceras f. scotica* sensu Schröder (1900): 15, Pl. 1, Fig. 17g; *non C. tripos scoticum* Schütt (1892): 302, Figs. 76 IVc and 91 IV (Fig. 76 IVc = *C. macroceros*, Fig. 91 IV unidentifiable with certainty—Jörgensen (1911) considered it as possibly *C. intermedium* (Jörg.) Jörg. (= *C. tenue*)).
? *C. tripos tergestinum* sensu Karsten (1906): 144, Pl. 21, Fig. 24. (Jörgensen (1911) and Schiller included this in the synonomy of '*var. protuberans*'. The antapical horns are very short, with closed pointed tips, the left horn MBC degree co-ordinate is 90° and the right horn has only a very slight initial backward curvature, so that it might be a badly drawn specimen of *C. tripos* (Müller) Nitzsch); *non C. tripos var. tergestina* Hensen (= *C. longipes* (Bail.) Gran).

*(Scales given by these authors could be inaccurate, as is certainly the case in Schröder (1900). Okamura has confused *C. tenue* and *C. massiliense* (as has Karsten (1907): 412), and the correct identification of his figures depends upon their girdle diameter. Some of the diameters of figures of Schröder (1906) and Karsten are far larger than any encountered in NGY Agulhas current specimens.)

Diagnosis: Differs from *var. carriense* in that the left horn degree co-ordinate with the 150 μ radius co-ordinate is > 130°. (Differs from *f. armatum* in that spines are not always present along the lower margins of the antapical horns, and if they are present, these spines decrease in size distally, so that at the level of the base of the apical horn they are absent or minute.)

Taxonomic history and present treatment: Karsten (1906) described his two new

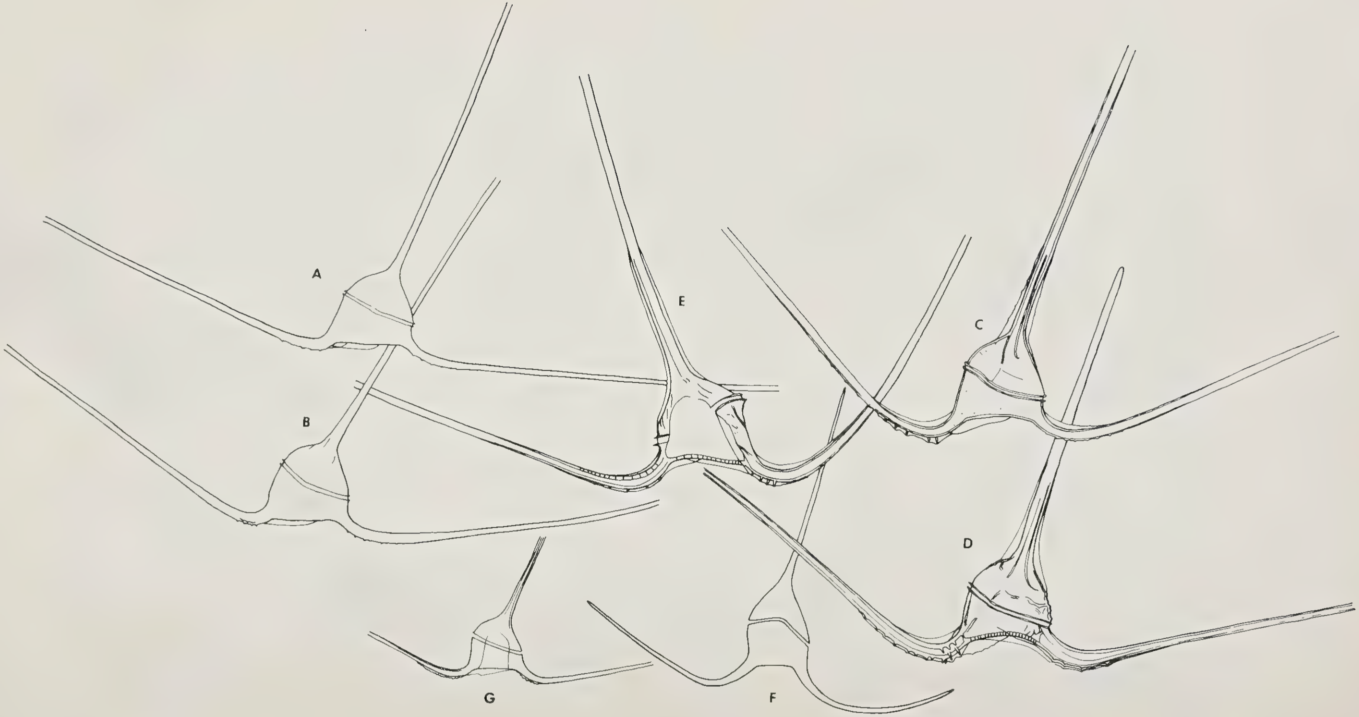


FIG. 16.

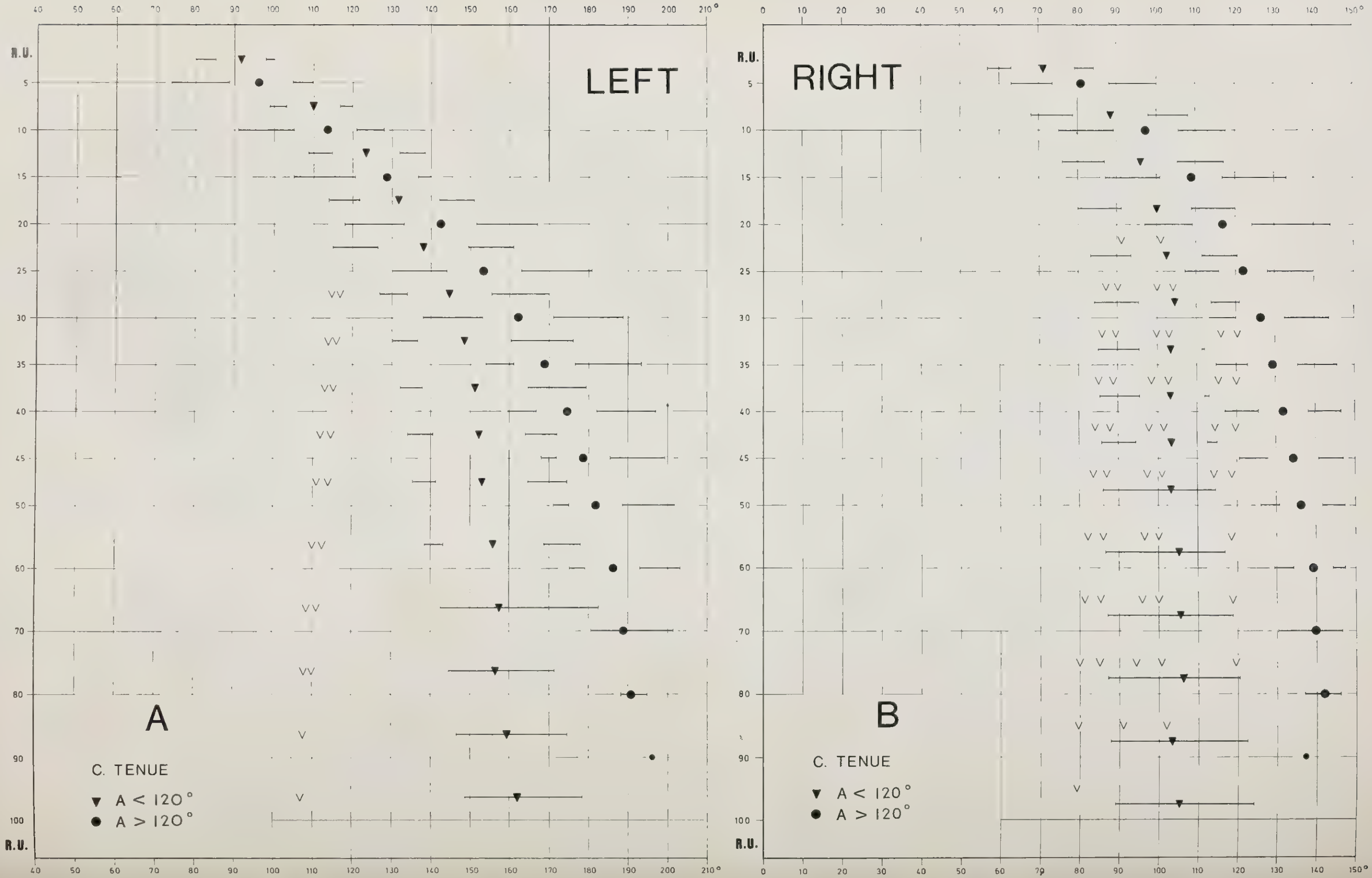
C. massiliense var. carriense (Gour.) Rein.: **A–E**, specimens from Agulhas current NGY samples, thecal wall shown in optical section and surface view, horns incompletely shown; measurements for each specimen given in the following order: girdle diameter, left horn degree co-ordinates with 15 μ, 150 μ and 300 μ radius co-ordinates; **A** 66 μ, 57°, 105°, 110°; **B** 69 μ, 68°, 116°, 120°; **C** 69 μ, 50°, 115°, 128°; **D** 78 μ, 50°, 114°, 120°; **E** 75 μ, 56°, 119°, 137°; **F**, Gourret's iconotype of "*C. carriense*" (1883, Pl. 4, fig. 57); **G**, Cleve's iconotype of "*C.* (*tripos var.?*) *volans*" (1900, Pl. 7, fig. 4).

species *C. tripos protuberans* and *C. tripos macroceroides* (treated by Jörgensen as *var. massiliense*) thus: "Man seiht die Scheitellinie fast oder doch nur mit geringem Absatz auf das linke Antapikalhorn übergehen, während das rechte deutlich über diese Grenze nach unten verstösst . . . Sie mogen als *Ceratium tripos protuberans* n. sp. benannt . . . Fig. 27a–g, Taf. XXII . . . *Ceratium tripos macroceroides* n. sp. Fig. 28, Taf. XXII . . . welches bereits beide Antapiklhörner über die Scheitellinie hinausstrekt, aber noch nicht die Knickung im Ansatz des linken Antapikalhornes zeigt, die für *macroceras* selbst charakterisch ist."

Jörgensen (1911) distinguished between *C. massiliense* and '*C. massiliense var. protuberans*' thus: in '*var. protuberans*', which is generally slightly larger, the left horn is laterally directed from its inception and its base is not, or indistinctly, delimited from the base of the hypotheca; the angle made by the bases of the left horn and the hypotheca is larger, mostly 180°; the distance *B* is small; the proximal parts of the antapical horns are very stout, the distal parts frequently long and thin; the base of the hypotheca is mostly distinctly convex in ventral view; the profile of the epitheca is more convex; the left profile of the hypotheca is almost straight; the theca is usually thickened and the apical horn is mostly somewhat curved.

Using these criteria, however, it is impossible to distinguish two distinct taxa, as Jörgensen did, in the specimens depicted in Karsten's Figs. 27 and 28. In Fig. 27a and c–g, the left horn MBC degree and radius co-ordinates are 90° and zero, while in Figs. 27b and 28, these co-ordinates are $< 90°$ and > 0; in all, the bases of the antapical horns are of a similar thickness; in Fig. 27d, the base of the hypotheca in ventral view is straight; there is little difference in body shape between Figs. 27 and 28, and the apical horn is not curved at the base in all specimens of Fig. 27; the specimens of Fig. 27a and b and Fig. 28 are similar in size, but those in Fig. 27c–g are larger. (Jörgensen did query the inclusion of Fig. 27a and b in '*var. protuberans*', but did not indicate to which other taxon they might belong.)

Peters (1932) considered that only *var. armatum* should be recognised as an infraspecific taxon of "*C. massiliense massiliense*", as it occurred in cooler waters than the other previously described components of this species, in which he included "*C. inflexum* (Gour.) Jörg." (= *C. trichoceros*), *C. deflexum* and '*var. protuberans*', all of which he found had the same distribution in the S. Atlantic. Steemann Nielsen (1934) appears to have regarded the subdivision of *C. massiliense* as unnecessary, for he found many intergrades. He found only "*a-macroceroides*-like" forms in the warmest parts of the S. Equatorial current and only *protuberans*- and *armatum*-like forms in temperate waters off New Zealand, but mixed "*macroceroides-protuberans*" populations in other warm parts of the S. Pacific. Graham & Bronikowsky (1944) reported nine recognisable varieties of *C. massiliense* in the Carnegie samples, with intergrades, de-


LEFT
RIGHT
A
B
R.U.
C. TENUE
▼ A < 120°
● A > 120°
40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210°
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150°
5 10 15 20 25 30 35 40 45 50 60 70 80 90 100

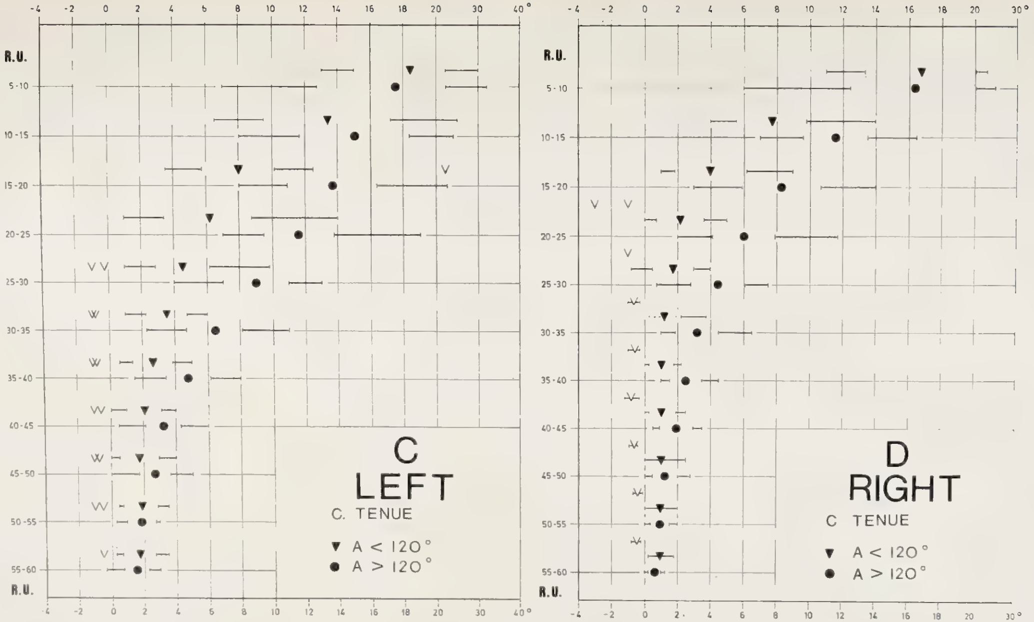


FIG. 17A–D.

C. tenue Ost. & Schm.: Antapical horn curvature in specimens from Agulhas current NGY stations. **A**, curvature of left horn expressed in degrees at 5 R.U. intervals from 5 to 50 R.U. and at 10 R.U. intervals from 50 to 100 R.U.; **B**, the same for the right horn; **C**, the rate of change of direction of curvature of the left horn expressed in degrees over 5 R.U. from 5–10 to 55–60 R.U.; **D**, the same for the right horn. A = right horn degree co-ordinate with 150 μ (50 R.U.) radius co-ordinate. See Key to Fig. 5; here the V's represent specimens with recurved horns.

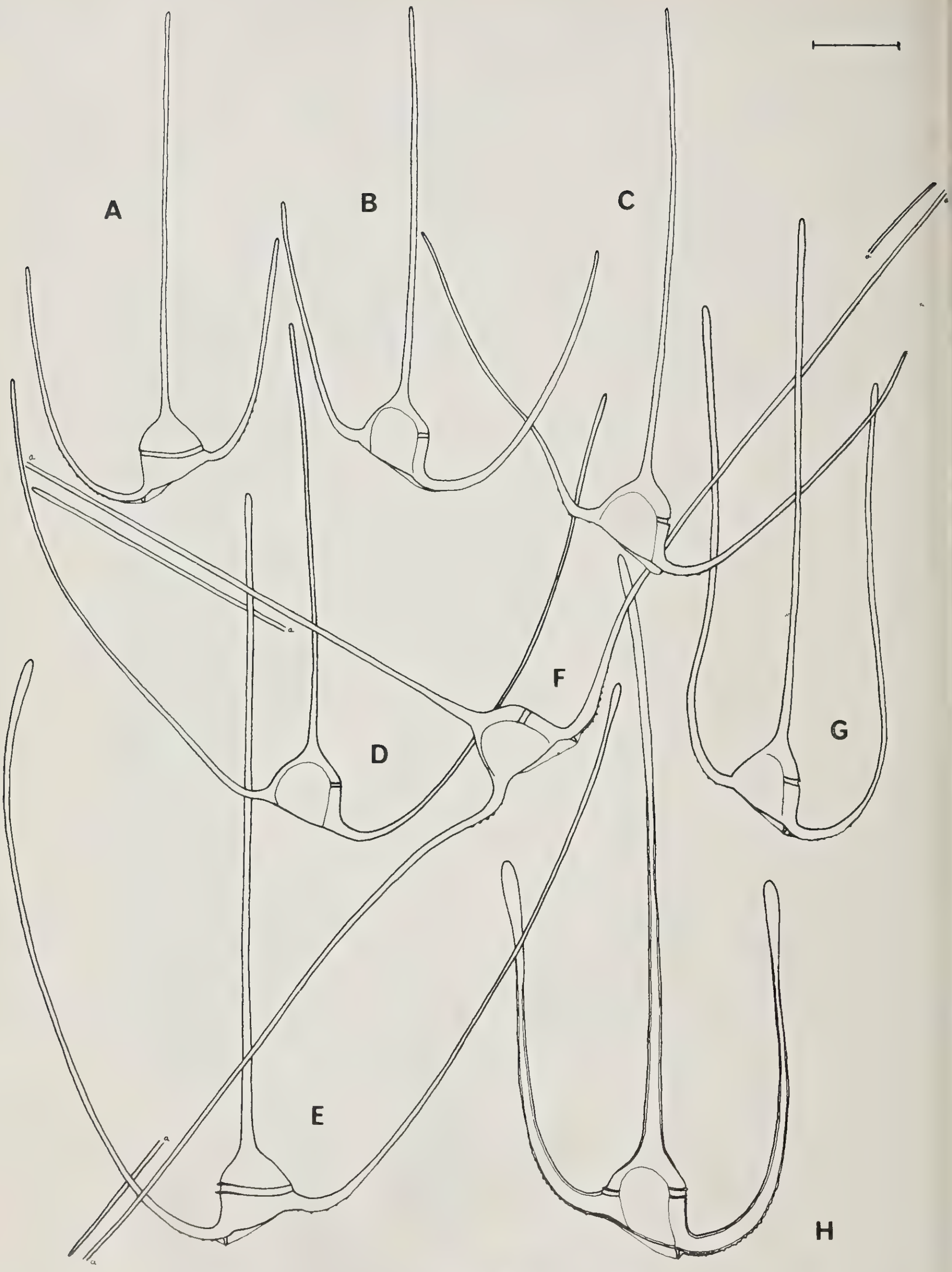


FIG 18.
C. tenue Ost. & Schm.: specimens from Agulhas current NGY stations; the scale line indicates 42 μ.

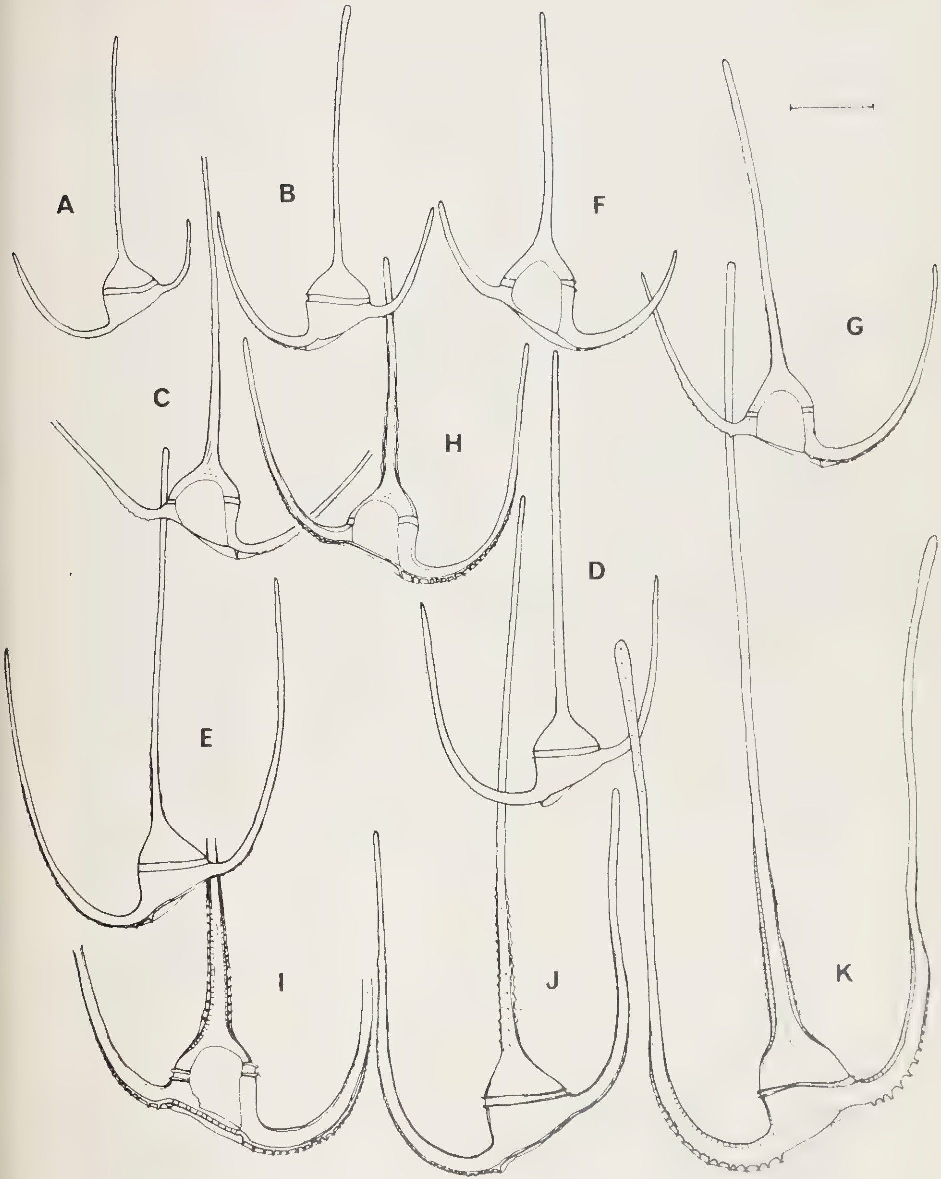


FIG. 19.
C. tenue Ost. & Schm.: specimens from Agulhas current NGY stations; the scale line indicates 42 μ.

scribed the habit of only eight, and named only *var. massiliense*, '*var. protuberans*' and *var. armatum*. They found no correlation between these varieties and hydrographic conditions. Sournia (1967) found that it was always possible to distinguish between *var. massiliense* and '*var. protuberans*' in his samples, from which *f. armatum* was absent.

In the Aghulas current NGY samples, specimens resembling Jörgensen's figures of both *var. massiliense* and '*var. protuberans*' were found. There was no discontinuity in the polar co-ordinate measurements of antapical horn curvature in these, in particular the left horn degree co-ordinates at MBC and with the 15 μ radius co-ordinate. Body shape, size, thickness of antapical horn bases and curvature of the apical horn varied independantly of these co-ordinates.

The maintenance of *var. protuberans* as a separate infraspecific taxon is indeed unwarranted.

Description: Antapical horn curvature: In specimens examined, antapical horns sometimes very slightly deflected ventrally, distal parts of horns sometimes slightly undulating, sometimes curving outwards. Polar co-ordinate measurements of horn curvature: *Left horn*: Varies from being latero-anteriorly directed at inception, when MBC degree and radius co-ordinates are 90° and zero, to having an initial backward curvature, with MBC co-ordinates varying to 63° and 42 μ, mostly 73–86° and 8–26 μ, when its base makes an indistinct to an obvious angle with that of the hypotheca; degree co-ordinate with 15 μ radius co-ordinate 55–100° ($>$ 100° in Karsten's *C. tripos intermedium var. hundhausenii*); with 105 μ, 120–149°, mostly 130–144°; with 150 μ, 134–174°, mostly 140–164°; with 300 μ, 145–184°; MRC occurs between 15 and 75 μ radius co-ordinates, (in only one case between 75 and 90 μ) and is 9–25°, mostly 10–17°; $\frac{L90}{D}$ 0,00–0,91, mostly 0,25–0,63; $\frac{B}{H}$ 0,00–0,81, mostly 0,22–0,50.
Right horn: Always curved backwards initially, making a rounded to a pointed angle with base of hypotheca; MBC degree co-ordinate 45–72°, mostly 50–65°, always less than in left horn, MBC radius co-ordinate 25–60 μ, mostly 33–50 μ, always greater than in left horn; degree co-ordinate with 15 μ radius co-ordinate 20–70°, mostly 30–55°, always less than in left horn; with 150 μ, 85–125°; with 300 μ, 95–125°; MRC occurs between 15 and 75 μ radius co-ordinates and is 10–22°, mostly 10–18°; $\frac{R90}{D}$ 0,69–2,20, mostly 0,90–1,75. Sum of left and right horn MRC's 20–39°, mostly 22–33°. (See Fig. 11.)

Dimensions: In NGY specimens: Girdle diameter 60–84 μ, mostly 63–73 μ; length hypotheca 36–54 μ; length epitheca 24–42 μ; length apical horn 132–645 μ (90 μ in one specimen, which could have been broken); angle made by projections of hypotheca base and girdle 22–34°. *From literature:* diameter 62–85 μ (Jörgensen 1911); 92 μ (Wang & Nie 1932); up to 81 μ (Steemann Nielsen 1934—he gives the range of measurements as 55–81 μ, but specimens $<$ 60 μ are here regarded as belonging to *C. tenue;* Nielsen found no correlation between diameter and temperature); 79 μ (Nie 1936); 61–122 μ (Steidinger & Williams 1970); length apical horn: up to 650 μ, angle between hypotheca base and girdle 27–33° (Jörgensen 1911). *Length antapical horns:* horn length variable and difficult to determine as horns often broken (or autotomised?); specimens seen in which antapical horns extend beyond level of top of apical horn and in others, antapical horns have closed rounded tips and extend to level of mid apical horn length. (See Fig. 10.)

Thecal ornamentation: Thecal walls smooth or thickened and ridged. Apart from sulcal list along left side of sulcus, up to three lists found along base of hypotheca: one, sometimes only list present, in angle between hypotheca and left horn, extending along hypotheca base for about two thirds of length of base and a little way onto base of left horn, sometimes continuing along lower margin of left horn, usually supported by small spines and gradually decreasing in width, to level of girdle; a second along base of sulcus; third in angle between base of right horn and hypotheca, extending up to halfway along hypotheca base and a very little way onto base of right horn, occasionally continuing long right horn as for left horn; sometimes additional lists found along lower edges of antapical horns, more rarely along right horn, situated along horns as already described. Margins of lists smooth to serrated; sometimes serrations of lists along hypotheca base thickened into denticles. Spines, if present along lower edge of antapical horns, sometimes stouter and longer in region of recurvature, diminishing in size to insignificance at level of base of apical horn. Occasionally, smooth margined lists, extending for a very short distance, found along upper margins of bases of antapical horns. Apical horn smooth, or ornamented at base with minute spines along plate sutures; sometimes a list present on one or both sides at base, seen in full dorsal or ventral view, with smooth to serrated margins, occasionally supported by spines. Tips of antapical horns sometimes slightly inflated.

Taxon Incertae Sedis

C. massiliense f. armatum (Karsten) Jörgensen (1920): 87.
Ex parte: Schiller (1937): 424, *non* Fig. 436b (= Jörgensen (1911) Fig. 146); Rampi (1939): 310, *non* Fig. 32; Wood (1954): 308, *non* Fig. 235b; Sournia (1967): 468, *non* Figs. 87, 88 (= Rampi Fig. 32, Peters (1932) Fig. 16a). (all *var. massiliense*).

C. massiliense var. armatum (Karsten) Jörgensen (1911) e.p.,: 67, *non* Pl. 8, Fig. 146; Peters (1932): 50, *non* Pl. 3, Fig. 16a; Graham & Bronikowsky (1944): 38, *non* Fig. 22L, (all = *var. massiliense*); Sournia (1966): 1982.
C. tripos var. macroceras f. armata Karsten (1905): 132, Pl. 19, Figs. 7, 8

C. tripos longipes var. cristata Karsten (1907): 413, e.p., Pl. 48, Fig. 12a, b *non* c (= *var. massiliense*).

Diagnosis: Distinguished by the presence of long spines along the lower edges of the antapical horns; these spines are still very prominent at the level of the base of the apical horn. Differs from specimens of *C. tenue* with very spiny antapical horns only on grounds of size, the girdle diameter here being > 60 μ.

The relationship between *C. massiliense var. massiliense* and the specimens described by Karsten as *C. tripos var. macroceras f. armata*, and *C. longipes var. cristata*, included in the synonomy of *var. armatum* by Jörgensen (1911) is problematic. Karsten's iconotype of *f. armata* shows a *var. massiliense*-like individual in which the left horn MBC degree co-ordinate is 90°, the antapical horns are not much longer than twice the body length and have tapered rounded tips. Both apical and antapical horns are ornamented for about three quarters of their length, beyond the level of the base of the apical horn, by lists which are supported by longish stout spines, which do not decrease much in size distally, are relatively long at the level of the base of the apical horn and are more like the spiny lists found in some specimens of *C. tenue*. Karsten later (1906: 146) considered *f. armata* to belong to "*C. tripos horridum*" (= *C. tenue*). However, the girdle diameter of Figs. 7 and 8, calculated from the somewhat confusing scale, appears to be larger than 65 μ, which is too big for *C. tenue*. The specimens of *var. cristata* of Fig. 12a, b, with a left horn MBC degree co-ordinate < 90°, have smooth lists along the proximal part of the apical horn and spiny lists along the base of the hypotheca as well as the lower margins of the antapical horns. The spines are also largish and more typical of *C. tenue;* they decrease in size distally, but are still quite long beyond the level of the base of the apical horn. The antapical horns are truncated. The specimen in Fig. 12c, described as having a newly formed antapical half, lacks any lists or spines on the antapical horns and hypotheca base.

Other specimens depicted by Karsten and attributed to *var. armatum* by Jörgensen are: "*C. tripos longipes f. ventricosa*" (1906) and "*C. tripos longipes*" (1907, Pl. 51, Figs. 12, 13). Later original figures of specimens referred to as *var.* or *f. armatum are* those of Jörgensen (1911), Peters (1932 Pl. 3, Fig. 16b) who depicts another specimen with virtually identical lists and spines as "*C. massiliense* . . . robust" in Pl. 1, Fig. 2b, Rampi (1939), Graham & Bronikowsky (1944) and Wood (1954). In none are the antapical horn lists supported by spines as described above. The apical horns are shown without lists, or with lists on either side of the base or proximal part, which are smooth, serrated or supported by spines. The proximal parts of the antapical horns have denticle-like spines or lists supported by spines, which are smaller than those depicted by Karsten in *f. armata* and '*var. cristata*'; they are longest in the region of recurvature and decrease in size distally, so that at the level of the base of the apical horn they are minute or absent. In one instance denticle-like spines are shown along the base of the hypotheca. In Karsten's figure of *f. ventricosa*, the antapical horns are similar to those depicted in his *f. armata*, while in the other figures mentioned, they are long or obviously truncated. *C. massiliense f. armatum* is mentioned, without any figures, by Jörgensen (1920), Gaarder (1954), Taylor (1967), and as *C. macroceras f. armata* by Nel (1968).

NGY specimens were found with horn ornamentation as just described, save that in no instances were the lists of the apical horns traversed by supporting spines. There was a complete gradation in antapical horn ornamentation to smooth antapical horns lacking lists along the lower margins.

Apart from Karsten's figures of *f. armata* and '*var. cristata*' (Fig. 12a, b) the specimens depicted in the literature and named or cited as "*C. massiliense f. or var. armatum* (Kars.) Jörg." are here regarded as specimens of *var. massiliense*. The true position of Karsten's *f. armata* and '*var. cristata*' is uncertain.

C. massiliense var. carriense (Gourret) Reinecke comb. nov. (See Figs. 13 F-H and 16.)

C. carriense Gourret (1883): 38, Pl. 4, Fig. 57; Jörgensen (1911): 68, Pl. 8, Fig. 147a, b; (1920): 89, Fig. 81; Schröder (1911): 646; Forti (1922): 68, Pl. 4, Fig. 54; Paulsen (1930): 90; Peters (1932): 50, Pl. 2, Fig. 10h; Schiller (1937): 425, Fig. 464a (= Jörgensen 147a), b; Rampi (1939): 310, Fig. 35; Graham & Bronikowsky (1944): 39, Fig. 22A; Wood (1954): 308; Halim (1960): 179; López (1966): 333, Figs. 47, 48; Steidinger & Williams (1970): 44, Fig. 13a, b.

C. cariense: Steemann Nielsen (1934): 26; (1939): 14.

C. carriense var. carriense: Sournia (1966): 1982; (1967): 470.

C. carriense f. eucarriense Böhm (1931a): 363.

C. carriense var. volans (Cleve) Jörgensen (1911): 70, Pl. 8, Figs. 148a, b, 149a, b; (1920): 90; Schröder (1911): 646; Pavillard (1916): 17, Pl. 1, Fig. 4; (1931): 89; Forti (1922): 69, Pl. 4, Fig. 55 (–Jörgensen Fig. 149a); Dangeard (1927): 378; Paulsen (1930): 90, Fig. 57A–D; Steenmann Nielsen (1934): 26, Fig. 64; Silva (1955): 172, e.p., Pl. 9, Figs. 6–8, *non* 5 (= *C. tenue* on account of size); Sournia (1966): 3; (1967): 470; Steidinger & Williams (1970): 44, Fig. 14a, b.

C. carriense f. volans (Cleve) Böhm (1931a): 363; Peters (1932): 50; Schiller (1937): 426, Fig. 465 (= Jörgensen Fig. 149a); Rampi (1939): 310, Fig. 37; Wood (1954): 309, Fig. 236a; Halim (1960): 79, Pl. 5, Fig. 11; (1963): 499.

C. carriense subsp. volans (Cleve) Margalef & Duran (1953): 42, Fig. 121.

C. carriense volans: López (1966): 333, Fig. 49.

C. carriense "*carriense-volans*"*:* Sournia (1966): 1982, (1967): 471.

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*(See comment under *var. massiliense*)

C. (*tripos var.*?) *volans* Cleve (1900a): 15, Pl. 7, Fig. 4.
C. tripos volans: Karsten (1906)*: 144, Pl. 21, Fig. 19a, b, 20, 20a.
C. volans (Cleve) Ostenfeld & Schmidt (1901): 168, Fig. 21; Pavillard (1905): 54, e.p., *non* Pl. 1, Fig. 1 (= *var. massiliense*); Pavillard (1931) Pl. 3, Fig. 5A; Okamura (1907)*: 130, e.p., Pl. 4, Fig. 18b, *non* a, c–e (18a = *C. tenue*, c–e = *var. massiliense*).
Non "*C. volans* forma": Schröder (1906)*: 363, Fig. 34 (= *var. massiliense*).
C. volans var. elegans (Schröder) Pavillard (1931) Pl. 3, Fig. 5B.
C. tripos volans var. elegans (Schröder) Karsten (1907): 409, Pl. 49, Fig. 18a, b.
C. elegans Schröder (1906): 364, Fig. 36.
C. carriense var. volans f. rectangulatum Jörgensen (1920): 90, Fig. 82, (= Jörgensen Fig. 148a).
C. carriense var. volans f. parallela Pavillard (1923): 916, Fig. C.
C. tripos volans f. strictissima Karsten (1906): 144, Pl. 21, Fig. 21.
C. tripos volans var. tenuissima Karsten (1907): 409, e.p., Pl. 49, Fig. 17b, *non* a (= *C. tenue*).
Non C. tripos volans f. recurvata Karsten (1906): 144, Pl. 21, Fig. 22 (= *C. tenue*).
C. carriense f. ceylanicum (Schröder) Jörgensen (1911): 70, Pl. 8, Fig. 150a, b; Böhm (1931a): 363; (1931b): 37; Peters (1932): 50; Steemann Nielsen (1934): 27; Schiller (1937): 427; Wood (1954): 309, Fig. 236b; Gaarder (1954): 11.
C. carriense var. ceylanicum (Schröder) Schröder (1911): 647.
C. ceylanicum Schröder (1906): 363, Fig. 35; Pavillard (1931): 92, Pl. 3, Fig. 6.
C. carriense f. hundhausenii (Schröder) Wood (1954): 309.
C. hundhausenii Schröder (1906): 364, Fig. 37; *non* Pavillard (1931) Pl. 3, Fig. 7 (= *C. macroceros*)
Non C. tripos intermedium var. hundhausenii Karsten (1907): 413, Pl. 50, Fig. 10 (= *var. massiliense*).
C. tripos var. massiliense Gourret (1883): 27, e.p., Pl. 1, Fig. 2a *non* 2 (= *var. massiliense*).
C. massiliense f. ellipticum Böhm (1931a): 362, e.p., Fig. 17b, *non* a, 18a, b, (Fig. 17b = *var. massiliense*).
C. patentissima Ostenfeld & Schmidt (1901): 168, Fig. 22.
C. patentissimum: Pavillard (1907): 226, Fig. 1A, B; Okamura (1907)*: 130, Pl. 3, Fig. 2a–c.
Non C. tripos patentissimum: Karsten (1906): 144, Pl. 21, Fig. 23, 23a (= *C. tenue*).
C. ostenfeldii Kofoid (1907b): 305, e.p., Pl. 26, Fig. 25, *non* 22–24 (22, 23 = *var. massiliense*, 24 = *C. macroceros*).
C. tripos macroceros: Entz (1902) e.p., Pl. 6, Fig. 42; Karsten (1907): 411, e.p., Pl. 49, Fig. 27d, *non* b (= *C. macroceros*).

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*(See comment under *var. massiliense*)

C. tripos macroceras var. crassa Karsten (1907): 411, e.p., Pl. 49, Fig. 27e, *non* a, c (a = *var. massiliense*, c = *C. macroceros*).
"*Ceratium* sp." Chun (1903): 64, Fig. a.

Diagnosis: Differs from *var. massiliense* (and *f. armatum*) in that the left horn degree co-ordinate with the 150 μ radius co-ordinate is < 130°.

Taxonomic history and present treatment: Jörgensen (1911) separated *C. carriense* from '*C. carriense var. volans*' on the grounds that in *C. carriense* the antapical horns are stouter, less spreading, usually more coarsely denticulate, with the right horn more evenly curved; the base of the hypotheca is more depressed between the antapical horns; the angle made by projections of the girdle and hypotheca base is larger; the left profile of the hypotheca is more oblique and the right profile of the epitheca is more convex.

In neither Gourret's figure of *C. carriense* nor Cleve's figure of *C. volans* can the spread of the antapical horns be determined, because only the proximal parts are shown. In both figures, the antapical horns are of similar thickness and the left profile of the hypotheca is oblique; in Cleve's figure, the antapical horns are ornamented with coarsely serrated lists, in Gourret's, lists and spines are absent; the right horn MRC occurs approximately between the 30 and 45 μ radius co-ordinates in Cleve's figure, and approximately between the 30 and 60 μ co-ordinates in that of Gourret.

As Gourret's specimen of *C. carriense* is drawn tilted, the true degree of depression of the hypotheca base between the antapical horns cannot be determined and polar co-ordinate measurements are not accurate. A comparison of Jörgensen's Fig. 147b of '*C. carriense*' and 148b of '*C. carriense var. volans*' shows an identical degree of depression of the hypotheca base, almost the same angle between the girdle and hypotheca base, and the right profile is more convex in Fig. 148b. In Paulsen's Figs. 57A and C of '*C. carriense var. volans*' the right horn is as evenly curved as in Gourret's Fig. 57.

Graham & Bronikowsky (1944) did not subdivide *C. carriense* into varieties because of the numerous intergrades. Steemann Nielsen (1939) wrote: "Es ist die ürsprungliche Varietät *volans* (Cleve), die ich unter dem Namen *C. carriense* angebe. Die ürsprungliche Hauptart ist wohl meistens zum Artenkomplex *C. massiliense* mitgerechnet worden." Sournia (1966, 1967), while retaining *var. carriense* and '*var. volans*', recognised the presence of intermediates, which he named, unconventionally, "*carriense—volans*". From the values of their left horn degree co-ordinates with the 150 and 300 μ radius co-ordinates, the specimens depicted in the literature which are cited by Sournia as intermediates, represent all three of the previously mentioned groups found in the NGY specimens.

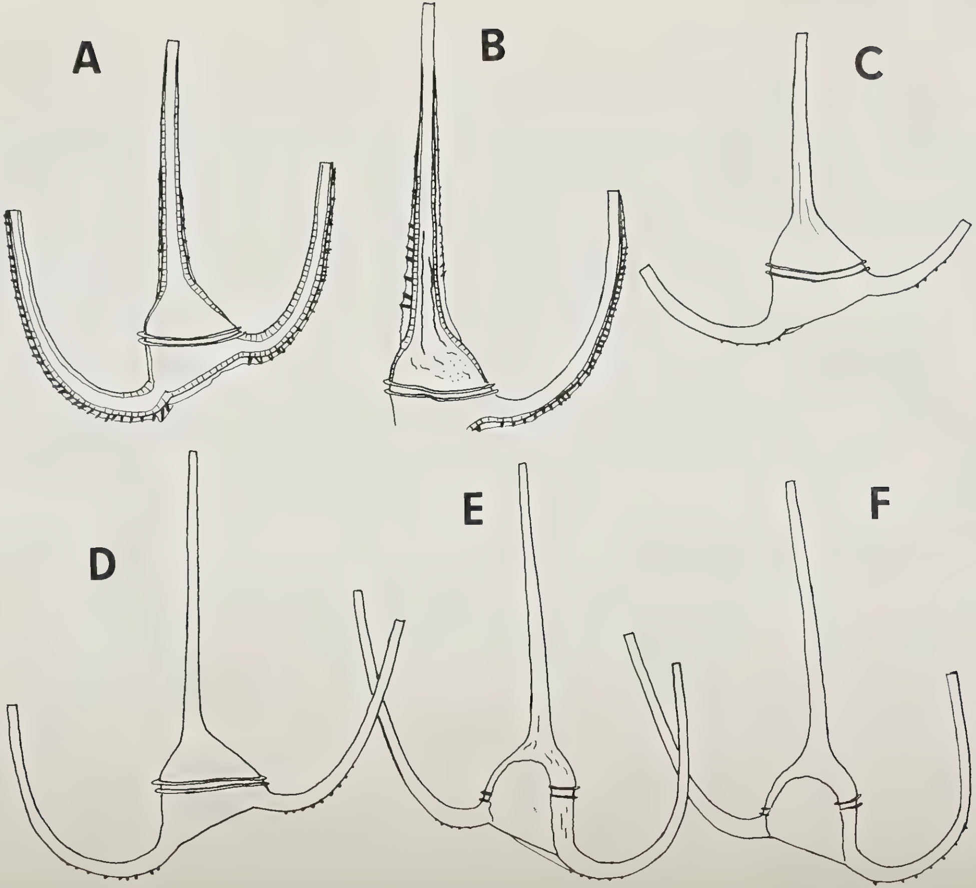

FIG 20
C tenue Ost. & Schm.: **A–C**, specimens from Agulhas current station NGY 41, (see page 70); **D–F**, specimens from Oslo Fiord. Girdle diameters: **A** 48 μ, **B** 54 μ, **C** 48 μ, **D** 54 μ, **E** 48 μ, **F** 48 μ.

It has been noted that the polar co-ordinate measurements of antapical horn curvature of specimens from the literature blurred the discontinuity between the two groups of NGY specimens approximating Jörgensen's concept of *C. carriense*. The subdivision of *var. carriense* into two taxa is indeed unjustified. It is of interest to note that, had two varieties been recognised, based on the left horn degree co-ordinate with the 300 μ radius co-ordinate, in specimens in which the left horn degree co-ordinate with the 150 μ radius co-ordinate was < 130°, the epithets '*carriense*' and '*volans*' would have had to to have been discarded.

Description: Antapical horn curvature: In specimens examined, both horns always curved backwards initially, left horn base making an indistinct to an obvious angle with the base of the hypotheca, usually the latter; horns long and disposition of distal parts very variable, often differing in right and left horns of same specimen; distal parts may be spreading to roughly parallel to the apical horn, sometimes recurved posteriorly, sometimes slightly undulating. *Polar co-ordinate measurements of curvature: Left horn:* MBC co-ordinates 60–84°, usually 60–80°, and 9–57 μ, mostly 15–45 μ; degree co-ordinates with 15 μ radius co-ordinate 50–85°, very rarely < 50°, mostly 50–70°; with 105 μ, 79–123°, mostly 95–115°; with 150 μ, 93–129°, mostly 100–125°; with 300 μ, 108–151°; MRC occurs between 15 and 75 μ radius co-ordinates, very rarely beyond 75 μ, and is 6–27°, mostly 7–15°; $\frac{L90}{D}$ 0,21–1,73, mostly 0,40–1,25; $\frac{B}{H}$ 0,20–1,42, mostly 0,30–0,90. *Right horn:* MBC degree co-ordinate 47–84°, mostly 50–80°, up to about 20° greater or less than in left horn; MBC radius co-ordinate very variable, 18–492 μ, mostly 37–150 μ, slightly less, to up to 480 μ greater, than in left horn; degree co-ordinate with 15 μ radius co-ordinate 20–80°, mostly 35–65°, up to 25° less, and 43° greater, than in left horn; degree co-ordinate with 105 μ radius co-ordinate 60–110°, mostly 65–95°; with 150 μ, 70–110°; with 300 μ, 75–125°; MRC occurs between 15 and 75 μ radius co-ordinates, very rarely beyond 75 μ, and is 3–14°, (20° recorded in one case), mostly 3–10°; $\frac{R90}{D}$ very variable, 1,30–10,48 (0,81 recorded in a single case). Sum of left and right horn MRC's 12–33°, (about 47° in Jörgensen's figure of '*C. carriense f. ceylanicum* (Schr.) Jörg.', (1911) Fig. 150). (See Fig. 11.)

Dimensions: In NGY specimens: girdle diameter 60–78 μ; length hypotheca 39–54 μ; length epitheca 21–42 μ; length apical horn 285–750 μ; angle made by projections of hypotheca base and girdle 19–31°. *From literature:* diameter 63–77 μ (Jörgensen 1911), up to 148 μ (Steidinger & Williams 1970—they give range of measurements as 56–148 μ, specimens < 60 μ in diameter are here treated as belonging to *C. tenue*); length apical horn 300–875 μ, angle between hypotheca base and girdle 20–27° (Jörgensen 1911). (See Fig. 10.)

Thecal ornamentation: As in *var. massiliense;* thecal wall generally not heavily thickened and extreme development of lists and spines not usually found;

specimens with initially very spreading antapical horns tend to have smooth horns and apart from the sulcal list, only a list between the base of the left horn and hypotheca.

Distribution: The distribution of *C. massiliense* in NGY Agulhas current stations is shown in Tables 1 and 2. In specimens from this area, there appeared to be no correlation between variation in size, antapical horn curvature and thecal ornamentation and temperature and neritic and oceanic conditions. Previous records for this area are those of Taylor (1967), as '*C. carriense f. carriense*' and '*f. volans*' and '*C. massiliense var. armatum*', "*C. massiliense* intermediate form" and '*C. massiliense var. macroceroides*', and Nel (1968) as '*C. carriense*', '*C. tripos volans*', '*C. tripos volans var. tennuissima*', '*C. macroceras f. armata*', '*C. macroceras var. crassa*', '*C. massiliense f. macroceroides*' and '*C. massiliense f. protuberans*'.

Var. massiliense is a neritic and oceanic warm water taxon, found in all oceans and the Mediterranean. Graham & Bronikowsky (1944) recorded it at an *in situ* temperature range of 10,6–29,5°C in the Pacific and N. Atlantic, where they described it as a tropical taxon, but very tolerant of temperatures below 19°C, most frequent in surface samples, one of the most common taxa of the genus, which could be displaced by ocean currents. In NGY samples, *var. massiliense* was not as common as thus indicated. Specimens with thicker thecal walls and more spinose horns, attributed to *f. armatum* by previous authors, and here treated as belonging to *var. massiliense*, were, in most cases, reported from cooler waters. Karsten's specimens *C. tripos macroceras f. armata* and *C. tripos longipes var. cristata*, provisionally treated as *f. armatum* were found in the S. Atlantic and S. Indian oceans at stations at 40° 31′ S., 15° 6,5′ E. and 41° 5,8′ S., 76° 23,5′ E.

Var. carriense has a distribution similar to that of *var. massiliense*, but is rarer. Graham & Bronikowsky found that it did not extend as far outside the tropical regions, and recorded it at an *in situ* temperature range of 12,5–29,5°C.

Ceratium tenue Ostenfeld & Schmidt (1901): 166, Fig. 18.

Jörgensen (1911): 77, Pl. 9, fig. 163; Mangin (1912): 26, Fig. 11, p.p., (excluding large specimens which are *C. massiliense* (Gour.) Kars.); Pavillard (1916): 18, Pl. 1, Fig. 5; Forti (1922): 74; Steemann Nielsen (1934): 28, Fig. 69; (1939): 15; Nie (1936): 71, Fig. 34; Graham & Bronikowsky (1944): 43.

C. tenue var. buceros (Zach.) Jörgensen (1911): 78, Pl. 9, Figs. 164–166; Forti (1922): 74.

C. tenue f. inclinatum (Kof.) Jörgensen (1911): 78, Pl. 9. Figs. 162, 163.

C. tenue var. inclinatum (Kof.) Graham & Bronikowsky (1944): 43, Fig. 26C.

C. tenue var. tenuissimum (Kof.) Graham & Bronikowsky (1944): 43, Fig. 26D.

C. buceros f. tenue (O. & S.) Schiller (1937): 415, Fig. 456a, b (a = Böhm (1931a) Fig. 20, b = Jörgensen (1911) Fig. 163); Rampi (1942): 226, Fig. 9; Gaarder (1954): 10; Wood (1954): 302, Fig. 231a; Halim (1960): 179, Pl. 5, Fig. 16; (1963): 499, Fig. 33; Cassie (1961): 18; Nel (1968); Thorrington Smith (1969); Steidinger & Williams (1970): 44, Fig. 12.
C. buceros var. tenue (O. & S.) Wood (1963): 5.
C. buceros tenue: López (1966): 333, Fig. 41.
C. horridum subsp. buceros var. tenue (O. & S.) Jörgensen (1920): 97; Silva (1949): 362; Margalef & Duran (1953): 42, Fig. 12g–i.
C. horridum var. tenue (O. & S.) Böhm (1931a): 365, Fig. 20; (1931b): 41.
? *C. horridum subsp. tenue:* Dangeard (1927): 379, *non* Fig. 43a (= *C. trichoceros* (Ehb.) Kof.).
? *C. tripos var. horrida* Cleve (1897): 302, Pl. 1, Fig. 4.
C. horridum (Cl.) Gran (1902): 194; Ostenfeld (1903): 584; Okamura (1907): 129, p.p., *non* Pl. 4, Fig. 23 (probably a freak specimen of *C. macroceros* (Ehb.) Cl. as ratio $\frac{B}{H}$ about 1,29); Jörgensen (1920)*: 96; Lebour (1925)*: 155, Pl. 34, Fig. 2; Dangeard (1927)*: 378; Paulsen (1930)*: 91, Fig. 59A–C; Böhm (1931a)*: 365; (1931b)*: 41, Peters (1932)*: 51; Schiller (1937)*: 413, Fig. 455a, b *non* c (a after Peters, b = Jörgensen (1911) Fig. 176, c, original, = *C. massiliense* as diameter about 70 μ); Silva (1949)*: 362, e.p., (not specimens with diameter $\geq 60\ \mu$); Gaarder (1954)*: 12; Wood (1954)*: 300, Fig. 230a, b; (1963)*: 10; Halim (1960)*: 180, Pl. 5, Fig. 10; (1963)*: 499, Fig. 32; Cassie (1961)*: 18, Pl. 7, Fig. 12; López (1966)*: 333, Figs. 42, 43; Taylor (1967)*: 463; Nel (1968); Steidinger & Williams (1970): 46; *non* Wailes (1928)* Pl. 1, Fig. 1 (= *C. longipes* (Bail.) Gran).
C. horridum subsp. α horridum: Jörgensen (1920): 97.
C. (*macroceros subsp.*) *horridum:* Gran (1902): 193 (in key).
C. horridum var. horridum: Graham & Bronikowsky (1944): 42, Figs. 24C 1, 25A–C, G *non* E, F (= *C. massiliense* on account of size); Sournia (1966): 1982; (1967): 476, Fig. 91; Paredes (1969/70): 43, Pl. 21, Fig. 146.
C. horridum var. genuina Gran (1902): 195.
C. horridum var. genuinum: Dangeard (1927): 379.
C. horridum α genuinum: Jörgensen (1920): 97, Fig. 86.
C. horridum subsp. horridum var. genuinum: Jörgensen (1920): 97.
C. horridum f. genuina (Gran) Ostenfeld (1903): 585.
C. horridum f. genuinum: Peters (1932): 54.
"*C. horridum* (Cl.) *f. typica* Gran" Ostenfeld (1903): 585, Figs. 136. 137.
C. horridum f. laevis Okamura (1907): 129, p.p., Pl. 4, Fig. 21e *non* d, f h (g *C. contortum* (Gour.) Cl., d, f, h = *C. massiliense* on account of size).

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* Species cited as *C. horridum* Gran; by Dangeard as *C. horridum* (Gran) Jörg

C. tripos β macroceros f. intermedia Jörgensen (1899): 42, Pl. 1, Fig. 10.
C. horridum var. intermedia (Jörg.) Gran (1902): 195.
C. horridum subsp. horridum var. intermedia: Jörgensen (1920): 97.
C. horridum f. intermedia (Jörg.) Ostenfeld (1903): 585, Fig. 139; Okamura (1907): 129, p.p., Pl. 4, Fig. 21b *non* a, c (= *C. massiliense* on account of size).
"Intermediate between *C. horridum f. typica* and *f. intermedia*": Ostenfeld (1903): 585, Fig. 138.
C. intermedium (Jörg.) Jörgensen (1905): 111; (1911): 83, Pl. 10, Figs. 174–176; Pavillard (1905): 53; (1907): 228; (1931): 91; Paulsen (1907): 22; (1908): 83; Ostenfeld (1931): 615; Wang (1936): 163, Fig. 31; Silva & Pinto (1948): 172, Pl. 2, Fig. 14; ?Wang & Nie (1932): 300, Fig. 13 (diameter given as 60 μ—most likely is *C. massiliense*).
C. intermedium f. spinifera Paulsen (1907): 22; (1908): 83, Fig. 111 (= Ostenfeld (1903) Fig. 136).
C. intermedium f. typica Paulsen (1907): 22; (1908): 83, 84, Fig. 112 (= Ostenfeld (1903) Fig. 139).
C. intermedium f. frigida Paulsen (1907): 22, Fig. 32; (1908): 83, 84, Fig. 113.
C. horridum subsp. horridum f. frigida (Pauls.) Jörgensen (1920): 97 (also referred to by Jörgensen (l.c.) as *f. gracilis*).
C. batavum Paulsen (1907): 23, Fig. 33a–d; (1908): 84, Fig. 114.
C. intermedium f. batavum (Pauls.) Jörgensen (1911): 83, 124, Pl. 10, Fig. 177.
C. intermedium var. batavum (Pauls.) Ostenfeld (1931): 616.
C. horridum subsp. horridum var. batavum (Pauls.) Jörgensen (1920): 97.
C. buceros Zacharias (1906): 551, Fig. 15; Schiller (1937): 415; Wood (1954): 301; Cassie (1961): 18; Nel (1968).
C. tripos buceros (Zach.) Karsten (1907): 409, Pl. 48, Fig. 16, *non* Pl. 51, Fig. 8 (= *C. recurvum* (Jörg.) Reinecke).
C. horridum subsp. buceros (Zach.) Jörgensen (1920): 97, Fig. 90; Dangeard (1927): 379.
C. horridum subsp. buceros f. buceros (Zach.) Jörgensen (1920): 97; Silva (1949): 362, Pl. 7, Fig. 6.
C. horridum f. buceros: Böhm (1931a): 365.
C. horridum var. buceros (Zach.) Sournia (1966): 1982; (1967): 477, Fig. 95.
C. horridum "horridum—buceros" Sournia (1966): 1982; (1967): 480, Fig. 92.
C. horridum "horridum > buceros" Sournia (1967): 480, Fig. 94.
C. horridum "buceros > horridum" Sournia (1967): 480, Fig. 93.
C. inclinatum Kofoid (1907b): 303, Pl. 25, figs. 16–21; Pavillard (1931): 91.
C. tripos inclinatum (Kof.) Karsten (1907): 412, 413, Pl. 49, Figs. 19, 20.
C. horridum subsp. buceros f. inclinatum (Kof.) Jörgensen (1920): 97, (as a form of *subsp. buceros var. tenue*), Fig. 88 (= Jörgensen (1911) Fig. 162a); Silva (1949): 362, Pl. 7, Fig. 5.

C. horridum f. inclinatum: Böhm (1931a): 365; (1931b): 41, Fig. 36d, e.
C. buceros f. inclinatum (Kof.) Schiller (1937): 415, Fig. 456c (= Jörgensen (1911) Fig. 162a); Rampi (1942): 226, Fig. 16; Gaarder (1954): 10; Wood (1954): 302, Fig. 231b, c; Silva (1956): 22; Halim (1960): 179, Pl. 5, Fig. 17; Taylor (1967): 462; Nel (1968).
Non C. tripos inclinatum var. minor Karsten (1907): 412, Pl. 51, Fig. 9a, b (probably = *C. declinatum* Kars.).
C. mollis Kofoid (1907b): 304, Pl. 27, Fig. 29.
C. molle Kof.: Jörgensen (1911): 81, Pl. 9, Fig. 170, Pl. 10, Figs. 171, 172; Schröder (1911): 647; Pavillard (1916): 19; (1931): 90; Forti (1922): 75; Steemann Nielsen (1934): 28, Fig. 71; (1939): 15; Wang (1936): 162, Fig. 30.
C. horridum subsp. buceros var. molle (Kof.) Jörgensen (1920): 97, Fig. 87; *non* Margalef & Duran (1953): 42, Fig 12j, k (= *C. massiliense* on account of size).
C. horridum subsp. buceros var. molle: Silva (1949): 362, Pl. 7, Fig. 7, Pl. 9, Fig. 13.
C. horridum var. molle: Böhm (1931a): 365; (1931b): 41, Fig. 36a–c; Graham & Bronikowsky (1944): 42, Figs, 23I, K, 25D.
C. buceros f. molle (Kof.) Schiller (1937): 417, Fig. 457a (= Jörgensen (1911) Fig. 170); Rampi (1942): 226, Fig. 17; Gaarder (1954): 10; Wood (1954): 303, Fig. 231g; Silva (1956): 22; Halim (1960) Pl. 5, fig. 13; Cassie (1961): 18, Pl. 7, Fig. 14.
C. buceros var. molle (Kof.) Wood (1963): 5.
C. buceros molle: López (1966): 333, Fig. 39, 40.
C. tenuissimum Kofoid (1907b): 307, Pl. 29, Figs. 32, 33; Paulsen (1930): 93, Fig. 60A, B.
C. tripos volans var. tenuissima (Kof.) Karsten (1907): 409, Pl. 49, Fig. 17a *non* b (= *C. massiliense var. carriense* (Gour.) Reinecke, on account of size).
C. horridum subsp. buceros f. tenuissimum (Kof.) Jörgensen (1920): 97, Fig. 89 (= Jörgensen (1911) Fig. 166 under *C. tenue var. buceros*).
C. horridum f. tenuissimum (Kof.) Böhm (1931a): 365.
C. buceros f. tenuissimum (Kof.) Schiller (1937): 417, Fig. 457a (= Jörgensen (1911) Fig. 166); Rampi (1942): 227, Fig. 18; Gaarder (1954): 10; Wood (1954): 303, Fig. 231h; Halim (1963): 499, Fig. 34.
Non C. tripos macroceras var. tenuissima n. var. Karsten (1907): 411, Pl. 49, Fig. 28 (= *C. macroceros*).
C. horridum subsp. buceros var. denticulatum Jörgensen (1920): 97, Fig. 91.
C. horridum subsp. buceros f. denticulatum (Jörg.) Silva (1949): 352, Pl. 7, Fig. 8.
C. denticulatum (Jörg.) Paulsen (1930): 93, Fig. 61.
C. horridum f. denticulatum (Jörg.) Böhm (1931a): 365; (1931b): 41, Fig. 36f, g.
C. buceros f. denticulatum (Jörg.) Schiller (1937): 417, Fig. 457b (= Paulsen (1930) Fig. 61); Rampi (1942): 227, Fig. 15; Wood (1954): 303, Fig. 231i; Halim (1960): 179; Cassie (1961): 18; Nel (1968); Thorrington Smith (1969).

C. claviger Kofoid (1907a): 170, Pl. 4, Fig. 27; Jörgensen (1911): 80, Pl. 9, Figs. 168, 169; Pavillard (1916): 18, Pl. 1, Fig. 6 (queried by him, as tips of antapical horns not shown); Steemann Nielsen (1934): 28, Fig. 70.

C. horridum subsp. buceros f. claviger (Kof.) Jörgensen (1920): 97 (suggested by him as a form of *subsp. buceros var. molle*).

C. horridum subsp. claviger (Kof.) Dangeard (1927): 379.

C. horridum var. claviger (Kof.) Graham & Bronikowsky (1944): 42, Fig. 23J, L.

C. horridum f. claviger (Kof.) Sournia (1967): 480.

C. buceros f. claviger (Kof.) Schiller (1937): 415, Fig. 456e (= Jörgensen (1911) Fig. 168); Rampi (1942): 226, Fig. 13; Wood (1954): 303, Fig. 231e, f; Silva (1955): 171, Pl. 9, Fig. 4; Halim (1960) Pl. 5, Fig. 12; Nel (1968).

C. leptosomum: Dangeard (1927): 379, Fig. 43c.

C. buceros f. leptosomum: Rampi (1942): 226, Fig. 19; Wood (1954): 302, Fig. 231d; ?Taylor (1967): 462; *non* Schiller (1937): 415, Fig. 456d (= Jörgensen (1911) Fig. 67).

Non C. leptosomum Jörgensen (1911): 80, Pl. 9, Fig. 167 (most like *C. macroceros*, ratio $\frac{B}{H}$ about 1,06).

? "*C. horridum subsp. buceros*, a degenerate form answering to *f. californiense* of *C. macroceros subsp. gallicum*": Jörgensen (1920): 98, Fig. 92 (= heteromorphic short horned specimen of uncertain affinity).

C. volans: Okamura (1907): 130, e.p., Pl. 4, Fig. 18a *non* b–e (= *C. massiliense* on account of size); *non C.* (*tripos var.*?) *volans* Cleve.

C. carriense var. volans: Silva (1955): 172, e.p., Pl. 9, Fig. 5 (specimen with small diameter).

C. massiliense: Peters (1932) e.p., Pl. 4, Fig. 17f.

C. tripos volans f. recurvata Karsten (1906): 144, Pl. 21, Fig. 22.

C. tripos flagelliferum f. angusta Karsten (1906): 146, e.p., Pl. 22, Fig. 33b *non* a (= *C. trichoceros*).

C. tripos flagelliferum var. angusta Karsten (1907): 410, 411, e.p., Pl. 49, Fig. 24b *non* a, c (a = *C. trichoceros*, b = *C. massiliense* on account of size).

? *C. flagelliferum var. filiformis* Okamura & Nishikawa (1904): 123, Pl. 1, Fig. 11.

C. tripos patentissimum: Karsten (1906): 144, Pl. 21, Fig. 23, *non C. patentissimum* O. & S.

C. tripos inversum Karsten (1907): 539 (= *C. tripos patentissimum* Karsten 1906).

? *C. tripos scoticum* Schütt (1892): 308, e.p., Fig. 91 IV *non:* 266, Fig. 76 IVc (= *C. macroceros*).

C. macroceras var. scotica (Schütt) Ostenfeld & Schmidt (1901): 167.

C. tripos macroceros f. undulata Schröder (1900): 16, e.p., Pl. 1, Fig. 17*l* *non* k, m (k = *C. massiliense*, m = *C. vultur var. pavillardii* (Jörg.) Reinecke).

C. macroceros: Lebour (1925): 155, e.p., Pl. 35, Fig. 1.

C. tripos macroceras f. graciosa Stüwe (1909): 274, Pl. 1, Fig. 9.

C. tripos sufflatum Stüwe (1909): 274, Pl. 1, Fig. 11.

Diagnosis: In the specimens examined, *C. tenue* differs from *C. massiliense* (Gour.) Kars. in that the girdle diameter is $< 60\ \mu$; *C. tenue* differs from *C. deflexum* (Kof.) Jörg. in that the right horn degree co-ordinate with the 15 μ radius co-ordinate is $> 45°$; *C. tenue* differs from *C. trichoceros* (Ehb.) Kof. in that the left horn MRC occurs before the 75 μ radius co-ordinate; (the single specimen of *C. tenue* in which the left horn MRC occurred beyond the 75 μ radius co-ordinate, differed from *C. trichoceros* in that the left horn degree co-ordinate with the 15 μ radius co-ordinate was $> 90°$ and the right horn MRC occurred before the 60 μ radius co-ordinate); C. tenue differs from *C. macroceros* (Ehb.) C. & L. in that the ratio $\frac{B}{H}$ is $< 0{,}60$.

Taxonomic history and present-treatment: C. tenue is the most variable species of Ceratium, and, as the synonomy shows, has had an extremely diverse taxonomic treatment. Jörgensen (1920) was the first to group its variants together in a single species "*C. horridum* Gran", consisting of two subspecies and a number of varieties and forms: *subsp. horridum* (also referred to by him as *α genuinum* Gran), with the infra-subspecific taxa *var. genuinum* Gran, *var. intermedium* (Jörg.), *var. batavum* (Pauls.) and *f. frigida* (Pauls.) and *subsp. buceros* (Zach.) with the infra-subspecific taxa *var. molle* (Kof.), *var. tenue* (O. & S.), *Var. denticulatum* Jörg., *f. inclinatum* (Kof.), *f. tenuissimum* (Kof.), *f. claviger* (Kof.) and *f. buceros*. This procedure was not universally adopted. Schiller (1937), for example, referred to "*C. horridum* Gran" and *C. buceros* Zach., the latter consisting of *f. tenue* (O. & S.) Jörg., *f. inclinatum* (Kof.) Jörg., *f. leptosomum* (Jörg.) Sch., *f. claviger* (Kof.) Jörg., *f. molle* (Kof.) Jörg., *f. tenuissimum* (Kof.) Jörg. and *f. denticulatum* (Jörg.) Sch. Sournia (1966, 1967) proposed a new treatment "outside the classical taxonomy", reducing the "*C. horridum*" complex to one species with three infraspecific taxa, *C. horridum var. horridum* (Cl.) Gran, *var. buceros* (Zach.) Sour. and *f. claviger* (Kof.) Sour. Intermediates between *var. horridum* and *var. buceros* were referred to as "*horridum—buceros*" "*horridum > buceros*" or "*buceros > horridum*".

An examination of the range of variation in specimens of *C. tenue* in the Agulhas current showed that it was quite impossible to delimit any infraspecific groups. An apparent discontinuity was found in the polar co-ordinate measurements of the curvature of the right horn, in that the degree co-ordinate with the 150 μ radius co-ordinate was $< 120°$ or $> 125°$, (see Fig. 17B). However, in more than half the specimens, the right horn did not extend to the 150 μ radius co-ordinate, and when the degree co-ordinate for this point was estimated in these, the discontinuity was eliminated. In some specimens, measurements of antapical horn curvature was further complicated by horn flexibility. (In three specimens of *C. tenue* seen from Oslo Fiord, the right horn degree co-ordinate with the 150 μ radius co-ordinate was estimated at between 120 and 130°). See Figs 18–20.

When treated as a single variable species, this species has always been referred to as "*C. horridum* (Cl.) Gran" or "*C. horridum* Gran". This is incorrect, for, following Article 60 of the International Code, which states that "In no case does a name or an epithet have priority outside its own rank", the species must be known as *C. tenue* Ostenfeld & Schmidt. This is fortunate, for the name "*C. tripos var. horrida* Cleve" might be regarded as a *nomen confusum.*

Cleve (1897) wrote of his new taxon *C. tripos var. horrida:* ". . . resembles the *var. longipes*, but is remarkable for the spines on the horns and the tail . . .". In 1900, in the synonomy of "*C. tripos longipes* Bail.", Cleve (1900b), wrote: ". . . inclusive *var. horrida* Cl. l.c. Fig. 4 . . ." referring to his iconotype of *C. tripos var. horrida.* Jörgensen (1905) also considered that Cleve's iconotype represented *C. longipes* (Bail.) Gran, writing: "Cleve's figure . . . clearly shows the curved horn which is typical for *C. longipes* . . .". He maintained this view in 1911, commenting that this figure belonged to those illustrations of Cleve "which in themselves are impossible to interpret and consequently have only brought uncertainty and confusion". In 1920, he referred to "*C. horridum*

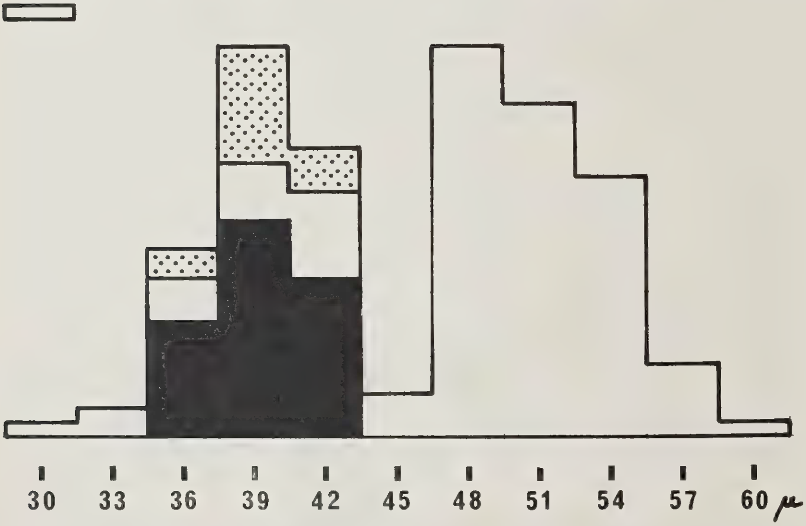

FIG. 21.

C. trichoceros (Ehb.) Kof.: Variation in girdle diameter in specimens from Agulhas current NGY samples. Black shading = presence of "basal kink" in left horn, white shading = absence of this kink, dotted shading = nature of base of left horn not recorded; single bar indicates one specimen.

Gran", noting that Cleve's figure of *C. tripos var. horrida* "may be this species, but is at least as likely to represent *C. longipes var. oceanicum* Ostf." Most authors after Jörgensen cited the taxon as "*C. horridum* Gran"; both Schiller (1937) and Wood (1954) writing in the synonomy: "*vix C. tripos var. horrida* Cleve".

C. batavum Paulsen is included in the synonomy of *C. tenue*, but the specimen of Figure 33b accompanying Paulsen's type description (1907), has a slightly curved apical horn.* A numerical assessment, using polar co-ordinate measurements of apical and antapical horn curvature, of the differences between *C. tenue*, *C. longipes* and *C. arcticum* (Ehb.) Cl. would be extremely useful. The last two species were not recorded from the Agulhas current samples. Graham & Bronikowsky (1944) combined *C. longipes* and *C. arcticum* into one species, *C. arcticum*.

The range of variation in antapical horn curvature in *C. tenue* is parallelled in *C. massiliense*. Size is the main criterion for the separation of the two species, for actual antapical horn curvature is very similar. (See Fig. 10.) In the Agulhas current samples, the girdle diameter in *C. tenue* was $\leq 54\ \mu$ and in *C. massiliense* $\geq 60\ \mu$, so that the species were always easily recognisable. A number of authors give girdle diameters for *C. tenue* in excess of 60 μ, and these are treated here as pertaining to *C. massiliense*. In general, specimens of *C. tenue* with spreading antapical horns and thin-walled thecae have a diameter of less than 50 μ (eg. Kofoid (1907b) gives diameters of 35–45 μ and 32–42 μ for *C. tenuissimum* and *C. inclinatum*), while in those with less spreading horns and thick thecal walls, diameters in excess of 50 μ are recorded (eg. Jörgensen (1911) gives a diameter of 42–57 μ for *C. intermedium*).

The problem of the taxon *C. massiliense f. armatum* (Kars.) Jörg. has been mentioned. In Karsten's figures (1905, Pl. 19, Figs. 7, 8), the spines supporting lists along the lower edge of the antapical horns, are prominent beyond the level of the base of the apical horn, as is usually the case in specimens of *C. tenue* with spiny antapical lists, and not otherwise the case in *C. massiliense*. Karsten himself later (1906) considered his specimen to belong to *C. horridum*, but its diameter, calculated from the scale of the figure, is in excess of 65 μ.

Variation in thecal ornamentation, horn curvature and relative length: The apical horn is straight or very slightly curved. The antapical horns, after the forward recurvature, vary from being extremely spreading, lying roughly at right angles to the apical horn, to lying parallel to it. Entire antapical horns with closed tapered tips, vary in length, from extending to a level about half the length of the body along the apical horn, to extending to roughly the length of the apical

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* Ostenfeld (1931) commented on '*C. intermedium var. batavum*': "... perhaps more likely belongs to *C. longipes*."

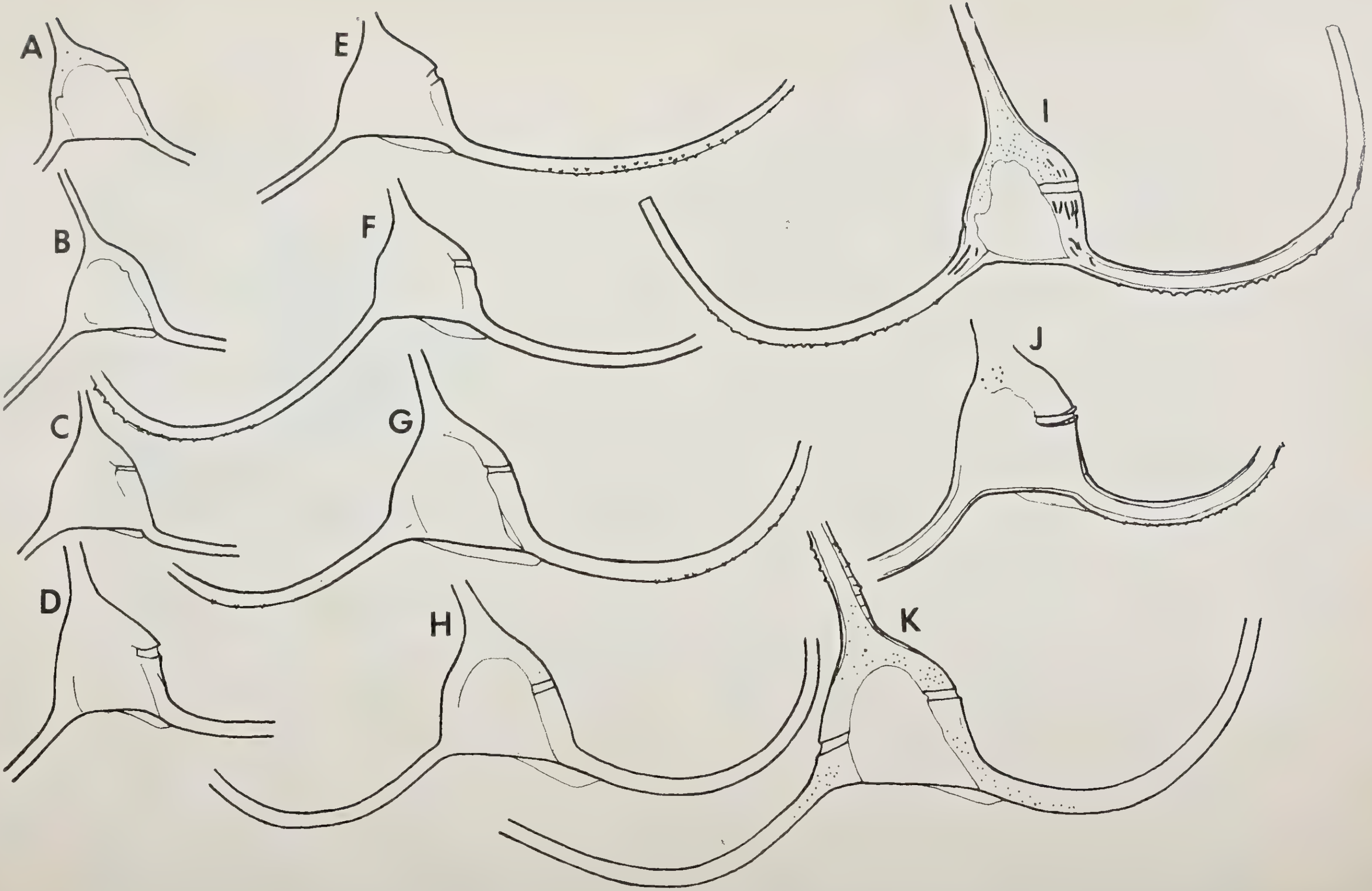


FIG. 22.

A–F, *C. trichoceros var. trichoceros* (Ehb.) Kof., **G–K**, *C. trichoceros var. contrarium* (Gour.) Sch.: Obvious left horn "basal kink" in **B**, **C** and **E**, slight kink in **D**; girdle incomplete in all save **K**; unusually thickened thecal wall in **I** and **J**, from station NGY 41 (see page 71); thecal wall in optical section and surface view in **I–K**. All specimens from Agulhas current NGY stations. Girdle diameters: **A** 39 μ, **B** 36 μ, **C** 39 μ, **D** 42 μ, **E** 42 μ, **F** 42 μ, **G** 51 μ, **H** 48 μ, **I** 48 μ, **J** 48 μ, **K** 57 μ.

horn. A list of varying width is almost always present between the base of the hypotheca and the base of the left horn, extending a varying distance along the base of the hypotheca, sometimes as far as the right side of the sulcus, and to the point of MBC on the horn, where it may be supported by a single spine.

A linear series of variations is found, with the short antapical-horned specimens in the middle. These generally have thin thecae and spineless horns, or a few minute spines along the lower margins of the antapical horns in the region of recurvature, and correspond approximately to the original concept of *C. tenue* O. & S. On the one side of the series of variations, the antapical horns become thicker proximally, longer, but never the full length of the apical horn, and less spreading to roughly parallel to the apical horn. The thecal wall may become thicker and ridged, with spines along the proximal part of the apical horn, sometimes in four rows along the plate sutures, and along the lower margins of the antapical horns. On the antapical horns, the spines vary from small denticles to prominent spines supporting lists, when the spines usually extend along the horns beyond the level of the base of the apical horn, gradually decreasing in size distally and lists may occur right across the base of the hypotheca; generally the longer the spines, the less the difference in their length at the base of the horn and at the level of the base of the apical horn. Similarly, the apical horn spines on the right and left sides may be very prominent, supporting lists, and extending along the horn for at least half its length.

The heaviest spines tend to be found in specimens in which the antapical horns are not very spreading, but not always. In specimens corresponding to *C. intermedium f. frigida* Pauls. for example, the horns are parallel to the apical horn, proximally stout and smooth, save for a few denticles on the left horn in the region of recurvature. Specimens are found either with the antapical horns broken, or with closed tapered ends; according to Nie (1936) "often with an obscure terminal pore". Sometimes, particularly noticeable in very thick-walled specimens, the distal parts of the antapical horns are thin-walled, more slender and flexible, often with the tips inflated, sometimes markedly so. This side of the linear series of variations may be described in terms of previously described taxa thus: *C. tenue* → *C. batavum* Pauls. → *C. tripos β macroceros f. intermedia* Jörg. → "*C. horridum f. typica Gran*" Ost. with *C. intermedia f. frigida* representing specimens with close antapical horns without heavy spines. It is specimens exhibiting the above range of variation which are found in colder waters. (See Figs. 18H, 19 and 20.)

On the other side of the linear series of variations, the antapical horns remain thin and increase markedly in length, becoming either very spreading, distally sometimes recurving outwards or inwards, or, more rarely, lying parallel to the apical horn. The distal parts of the antapical horns are flexible, the horn tips tapered-rounded and closed, sometimes slightly inflated. The thecal wall is generally thin, the horns smooth or with minute spines, sometimes supporting a narrow list along the region of recurvature of the antapical horns. In terms of previously described taxa, the linear series of variations is described thus: *C. tenue* → *C. inclinatum* Kof. → *C. buceros* Zach., *C. horridum subsp. buceros var. denticulatum* Jörg. and *C. tenuissimum* Kof., with *C. molle* Kof. representing the thin-horned specimens in which the antapical horns lie parallel to the apical horn. These forms are confined to warmer waters. (See Fig. 18 A–G.)

There is no discontinuity in this series of variations and further, specimens are found with smooth antapical horns more or less parallel to the apical horn, which are of an intermediate thickness, represented by *C. claviger* Kof., the first specimen figured with clavate horn tips, in this case, bifid in the right horn. (See Fig. 19 D.)

Polar co-ordinate measurements of antapical horn curvature: In some instances, distal parts of horns flexible, sometimes curved outwards; horns extend to 150 μ radius in less than half specimens examined. *Left horn:* MBC co-ordinates 65–90° and 0–15 μ; degree co-ordinate with 15 μ radius co-ordinate 70–110°, with 105 μ, 114–194°, with 195 μ, 109–203°; MRC occurs mostly between 15 and 30 μ radius co-ordinates, very rarely beyond up to between 75 and 90 μ co-ordinates and is 11–30°; $\frac{L90}{D}$ 0,00–0,77, mostly $< 0,60$; $\frac{B}{H}$ 0,03–0,56, mostly 0,10–0,40. *Right horn:* MBC co-ordinates 59–85° and 3–33 μ; degree co-ordinate with 15 μ radius co-ordinate 50–100°, with 105 μ, 85–146°, with 150 μ, 83–147°, with 195 μ, 82–147°; MRC occurs between 15 and 60 μ radius co-ordinates, mostly between 15 and 30 μ and is 8–23°; $\frac{R90}{D}$ 0,13–1,25, mostly 0,40–0,80, occasionally horn so spreading that 90° co-ordinate not reached. (See Fig. 17.)

Dimensions: In specimens examined: Girdle diameter 30–54 μ (48–54 μ in three specimens seen from Oslo Fiord); length body 33–60 μ; length hypotheca 15–33 μ; length epitheca 12–30 μ; length apical horn 96–735 μ. *From literature:* Diameter: 32–45 μ (Kofoid (1907)); 36–57 μ (Jörgensen 1911); 42–47 μ (Lebour 1925); 35–37 μ (Nie 1936); 32–43 μ (Steemann Nielsen 1934); average diameter of "*C. horridum*" 44 μ, of *C. tenue* 37 μ (Graham & Bronikowsky 1944); average diameter of "*C. molle*" 40 μ, of "*C. intermedium*" 58 μ (Wang 1936, probably including specimens of *C. massiliense*); length apical horn 150–450 μ (Jörgensen 1911).

Distribution: C. tenue is found in all oceans and the Mediterranean. The forms with thin horns on the one side of the line of variations are confined to warmer waters, while the forms with thicker horns have a very wide temperature tolerance and are cosmopolitan. However, the development of heavy spines along the horns appears to be associated with cooler waters, for there are no illustrated records of specimens of *C. tenue* with prominent spines from the tropics. Graham & Bronikowsky found both *C. tenue* and "*C. horridum*" to be shade species.

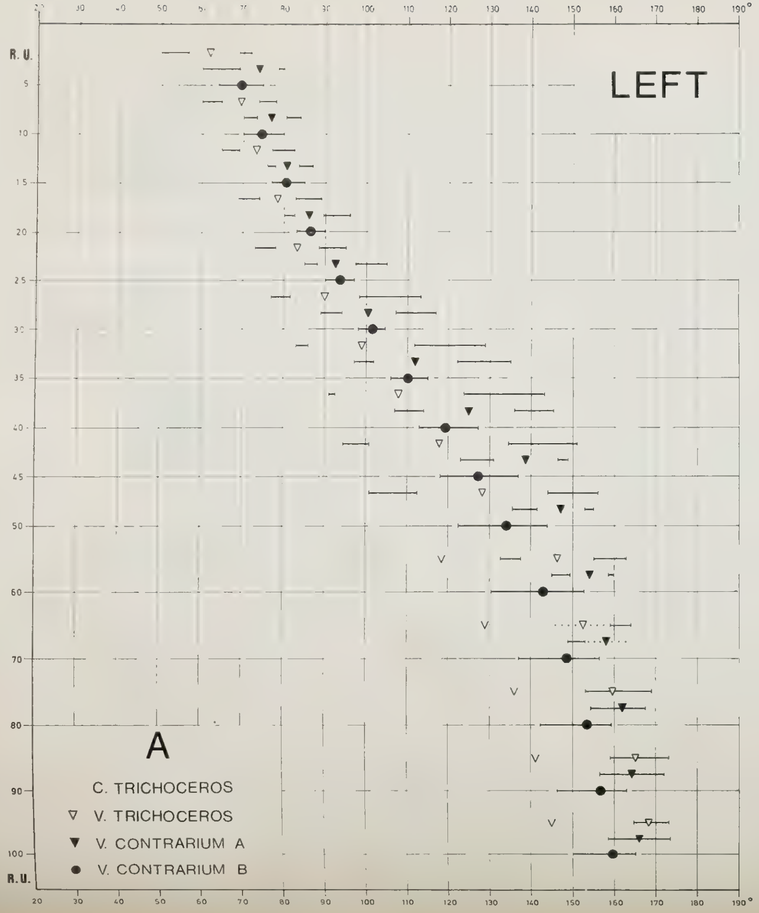
The distribution of *C. tenue* in the Agulhas current NGY stations is shown in Tables 1 and 2. In the Port Elizabeth line of stations, a wide range of variation was generally found at each station, but specimens with heavy spines were not common, except at the May cruise station 41, immediately off Port Elizabeth, where a number of specimens were seen with thick horns and thecal walls, generally with prominent spines supporting lists along the horns, such as in specimens from the Faeroes depicted by Ostenfeld (1903). Upwelling occurs off Port Elizabeth, and there is a North flowing current inshore of the Agulhas current, which originates in the vicinity of Cape Agulhas. It is more probable that these heavily spined forms developed as the result of an upwelling.

Cultur experiments on the effects of temperature on the different forms would be helpful in determining the exact nature of this variation.

Ceratium trichoceros (Ehrenberg) Kofoid (1908a): 362, Figs. 16-19.
Diagnosis: C. trichoceros is characterised by the fact that the left horn MRC occurs beyond the 75 μ radius co-ordinate. It differs from those specimens of other species of Subsection *Macroceras* in which the left horn MRC occurs beyond the 75 μ radius co-ordinate thus: from *C. macroceros* (Ehb.) Vanh. in that the left horn MBC degree co-ordinate is generally $\geq 70^\circ$; the few specimens of *C. trichoceros* in which this co-ordinate is $< 70^\circ$, but $\geq 65^\circ$, differ from the few specimens of *C. macroceros* in which this co-ordinate is $\geq 65^\circ$, in that the girdle diameter is $\leq 45\ \mu$, while in the specimens of *C. macroceros* it is $\geq 55\ \mu$; from the single specimen of *C. massiliense var. massiliense* (Gou.) Kars. recorded, in that the left horn degree co-ordinate with the 15 μ radius co-ordinate is $< 90^\circ$, and from the single specimen of *C. massiliense var. carriense* (Gour.) Rein. recorded, in that in specimens with a girdle diameter $> 45\ \mu$, the left horn MBC degree co-ordinate is $\geq 70^\circ$; from the single specimen of *C. tenue* O. & S. recorded in that the left horn degree co-ordinate with the 15 μ radius co-ordinate is $< 90^\circ$; from *C. deflexum f. sinensis* Rein. in that the right horn MBC degree co-ordinate is $> 40^\circ$.

Taxonomic history and present treatment: The two varieties of *C. trichoceros, var. trichoceros* and *var. contrarium* (Gour.) Sch. were first combined into one species by Schiller (1937), although the evidence suggests that earlier authors, in particular Cleve (1900a, b), had treated elements of both as belonging to a single taxon. Schiller's treatment was not universally adopted.

Sournia (1967) considered that the differences between the two were quite sufficient for their retention as separate species. The differences he listed, following Jörgensen (1911), were: in *C. contrarium* (Gour.) Pav., in comparison with *C. trichoceros*, the central body was larger, the left profile of the hypotheca more oblique and slightly concave, the epitheca was broader than high and the


LEFT
A
C. TRICHOCEROS
▽ V. TRICHOCEROS
▼ V. CONTRARIUM A
● V. CONTRARIUM B
R.U.
5
10
15
20
25
30
35
40
45
50
60
70
80
90
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70
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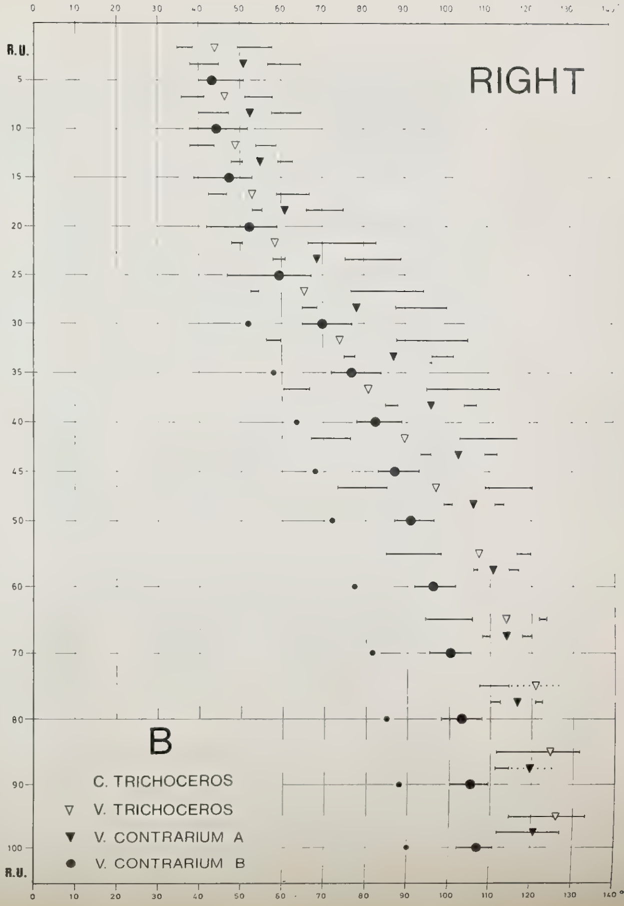
90
100
110
120
130
140
150
160
170
180
190°


RIGHT
B
C. TRICHOCEROS
▽ V. TRICHOCEROS
▼ V. CONTRARIUM A
● V. CONTRARIUM B
R.U.
5
10
15
20
25
30
35
40
45
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110
120
130
140°

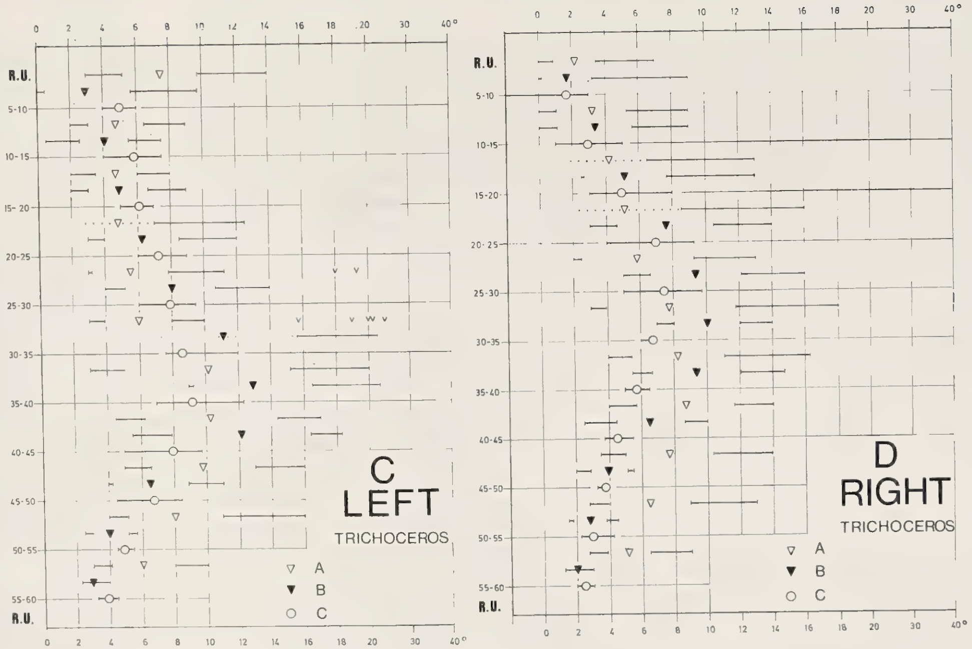

FIG. 23A–D.

C. trichoceros (Ehb.) Kof.: Antapical horn curvature in specimens from Agulhas current NGY stations. **A**, curvature of left horn expressed in degrees at 5 R.U. intervals from 5 to 50 R.U. and at 10 R.U. intervals from 50 to 100 R.U.; **B**, the same for the right horn; **C**, the rate of change of direction of curvature of the left horn expressed in degrees over 5 R.U. from 5–10 to 55–60 R.U., A = *var. trichoceros*, B = *var. contrarium* (Gourret) Schiller A, C = *var. contrarium* B; **D**, the same for the right horn. In *var. contrarium* B the right horn is more spreading than in *var. contrarium* A. See Key to Fig. 5 and page 81.

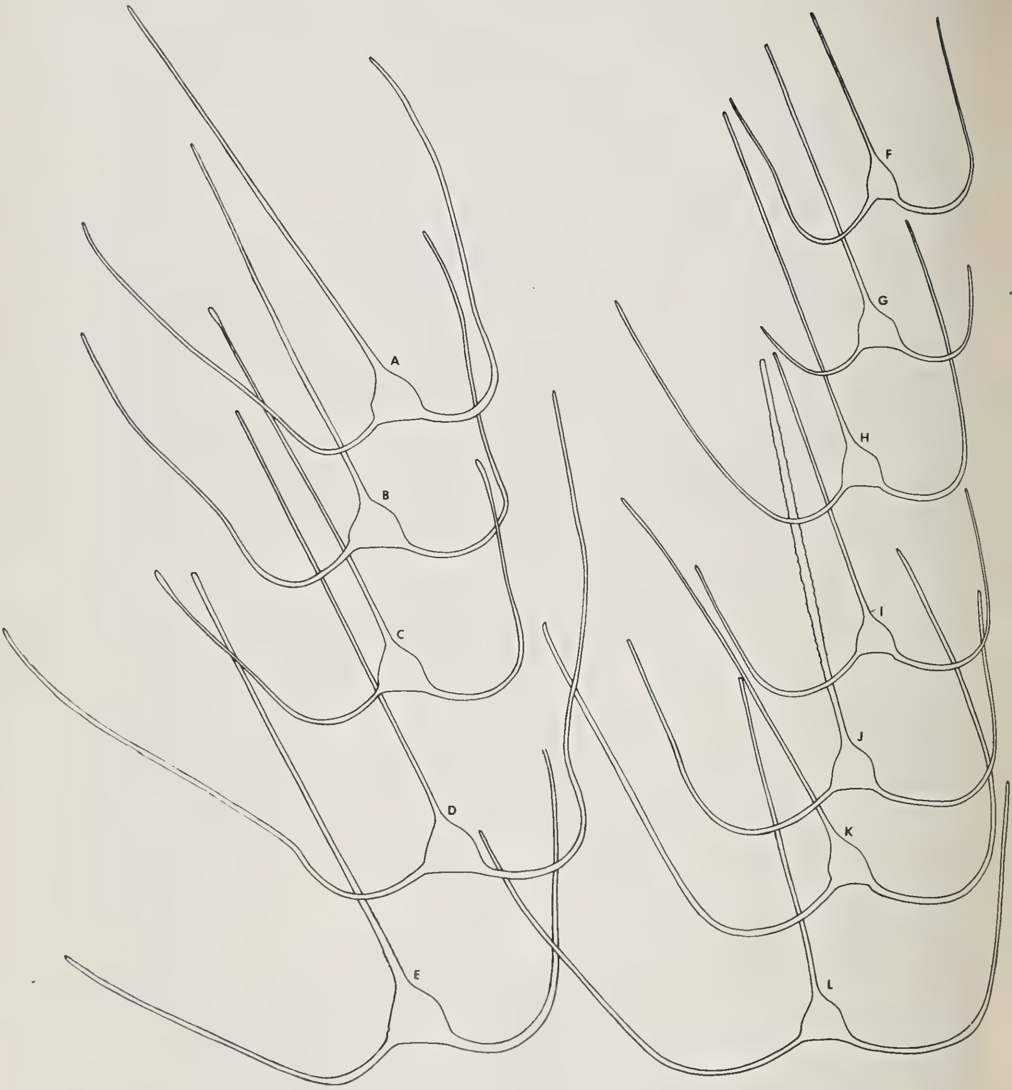

FIG. 24.

A–E, *C. trichoceros var. contrarium* (Gour.) Sch., **F–L**, *C. trichoceros var. trichoceros* (Ehb.) Kof.: Showing variation in antapical horn curvature; basal "kink" present in left horn of **I** and **K**; tips of antapical and apical horns inflated in **C**; apical horn inflated, with rows of spines along plate sutures in **J**; **E**, specimen with complete girdle and divergent antapical horns; girdle incomplete in others. All specimens from Agulhas current NGY stations. Girdle diameter: **A** 45 μ, **B** 48 μ, **C** 48 μ, **D** 54 μ, **E** 57 μ, **F** 30 μ, **G** 42 μ, **H** 39 μ, **I** 36 μ, **J** 42 μ, **K** 36 μ, **L** 39 μ.

girdle normally developed; the base of the left antapical horn was nearly continuous with the base of the hypotheca and lacked a basal "kink"; the recurvature of the right horn occurred about one or less than one girdle diameter along the horn, (in *C. trichoceros* about one to two girdle diameters); the antapical horns were not symmetrically curved, the right being more abruptly recurved and this recurvature occurring more anteriorly than in the left horn. Further there were some differences in the distribution of the two species.

A study of specimens depicted in the literature and from the Agulhas current NGY samples, indicates that, while two taxa can be identified, their separation into distinct species is not justified. The points of difference listed by Sournia are discussed below.

Examination of the girdle diameter in 140 NGY specimens, measured correct to 3 μ, showed a discontinuity in the measurements indicating two groups: the first with a diameter of 30–42 μ, the second with a diameter of 48–60 μ; in only three specimens was the diameter 45 μ. (Jörgensen (1911) gave the diameter of *C. trichoceros* as 37–48 μ and of '*C. inflexum* (Gour.) Kof.' (= *var. contrarium*) as 51–68 μ.) See Fig. 21.

Body shape varied regardless of size in both NGY specimens and those figured in the literature, and in all 75 NGY specimens measured, (and in Ehrenberg's iconotype), the width of the epitheca exceeded its height.

With regard to development of the girdle, it was sometimes incompletely developed in NGY specimens with a diameter exceeding 50 μ. When development of the girdle is incomplete, seen dorsally, the girdle lists are fully developed on the left side, becoming less developed to almost non-existant on the right. Seen ventrally, the girdle is fully developed on the left side of the sulcus, and completely absent or very faintly developed on the right. Sometimes the girdle lists are so slightly developed and the thecal wall is so thin, that the girdle is almost invisible at low magnification. It is often difficult to judge the nature of the girdle in figures from the literature. For example, in both Ehrenberg's iconotype and Cleve's figure (1900a) of "*C. flagelliferum*" the specimens are drawn seen ventrally, but the girdle is shown in dorsal aspect, extending right across the cell.

The basal "kink" of the left horn refers to a slight kink of the lower posterior edge of the horn about 3 μ from its origin adjacent to the hypotheca, the angle of the kink projecting outwards. In 16/50 NGY specimens with a diameter $\leq$ 42 μ, this kink was absent. It was never observed in NGY specimens with a diameter $\geq$ 45 μ. In all NGY specimens with this kink, the lower posterior edge of the left horn is markedly delimited from the hypotheca base, making an obvious angle with it. When the "kink" is absent, the delimitation of the base of the left horn from the base of the hypotheca is less marked to almost imperceptible. Generally, the larger the girdle diameter, the less apparent is this delimitation.

but NGY specimens with diameters of 42 μ and 51 μ were seen in which the angular delimitation between the base of the left horn and the hypotheca was virtually the same. (See Fig. 22.)

A comparison of the curvature of the right and left horns in NGY specimens using polar co-ordinates, showed that in the right horn, the MRC occurred at the same or at a shorter distance along the horn than the left horn MRC; only in one small diametered specimen did the MRC occur further along the right horn than the left, (also in Ehrenberg's iconotype). The situation of the MRC at a shorter distance along the right horn than along the left was more frequent in larger specimens. The ratio $\frac{\text{RMBC}}{\text{D}}$ never exceeded 1,75 in specimens with a diameter $\geq$ 45 μ. In the smaller specimens, this ratio was as large as 3,81, but individuals with low ratios were also found (eg. diameter 42 μ, $\frac{\text{RMBC}}{\text{D}}$ 1,27, diameter 39 μ, $\frac{\text{RMBC}}{\text{D}}$ 1,54). See Table 5.

It is clear that the above characters do indicate the existance of two taxa, but are insufficiently different in the two groups to warrant the establishment of two distinct species.

Description: Base of right horn always delimited from base of hypotheca, making a sharp or a rounded angle with it. *Base of left horn* in *var. trichoceros* generally makes an obvious angle with the base of the hypotheca and often has a slight "kink" about 3 μ from it; in *var. contrarium*, base of left horn mostly not markedly delimited from base of hypotheca.

Antapical horn curvature: Initially, proximal parts of horns very spreading; polar co-ordinate measurements of horn curvature in specimens examined: *Left horn:* degree co-ordinate with 15 μ radius co-ordinate 50–80°, generally $<$ 70° in *var. trichoceros* and $>$ 70° in *var. contrarium;* MBC degree co-ordinates 65–85°, ($<$ 70° recorded in only three specimens), mostly 72–78° in *var. trichoceros* and 75–82° in *var. contrarium;* MBC radius co-ordinate 22–75 μ, (95 μ recorded in one specimen), mostly 40–62 μ in *var. trichoceros* and 34–42 μ in *var. contrarium*. After initial change from zero point to 15 μ radius co-ordinate, two patterns of horn curvature are found: in the first, there is a gradual increase in rate of change of direction over successive 15 μ intervals up to zone of MRC; in the second, rate of change over 15 μ decreases beyond the 30 μ radius co-ordinate and then increases to a rate exceeding that between the 15 and 30 μ radius co-ordinates, up to zone of MRC; second pattern usually found in *var. trichoceros*, first in *var. contrarium*. MRC occurs beyond 75 μ radius co-ordinate, up to between 150 and 165 μ radius co-ordinates in *var. trichoceros*, generally not beyond 120 μ in *var. contrarium*, and is 8–25°, mostly 10–20°; degree co-ordinate with 150 μ radius co-ordinate very variable, 93–156° in *var. trichoceros*, 123–155° in *var. contrarium;* with 300 μ, values from 144–175° recorded in the few specimens seen with left horn extending to this level. *Right* *horn:* degree co-ordinate with 15 μ radius co-ordinate 25–60°, less than in left horn by up to 35°; curvature mostly of first type described above; MBC degree co-ordinate 50–70°, less than in left horn by up to 27°, mostly by 6–20°; MBC radius co-ordinates 37–120 μ (153 μ recorded in one specimen) greater than in left horn by up to 60 μ (by 101 μ in one specimen), (less than in left horn in one specimen), mostly 67–105 μ in *var. trichoceros* and 57–78 μ in *var. contrarium;* MRC occurs at same distance along right horn as along left, or at shorter distance, rarely further along horn; occurrence of MRC at shorter distance along right horn than along left more common in *var. contrarium;* degree co-ordinate with 150 μ radius co-ordinate 72–121°; with 300 μ, 90–135° in few specimens recorded (< 100° in a single specimen). See Fig. 23.

Beyond zone of MRC, rate of change of direction of curvature over successive 15 μ intervals decreases and right and left horns tend to lie roughly parallel to one another and apical horn; wall of distal parts of antapical horns tends to be thinner and distal parts may be slightly undulating, the latter often the the case in *var. contrarium*, rarely in *var. trichoceros.* (See Fig. 24.)

Spreading nature of proximal parts of antapical horns may be measured by radius co-ordinate with 90° co-ordinate: L90 45–135 μ, mostly 80–110 μ in *var. trichoceros*, mostly 60–80 μ in *var. contrarium;* R90 75–221 μ, mostly 105–115 μ in *var. trichoceros*, mostly 90–125 μ in *var. contrarium;* $\frac{\mathrm{L90}}{\mathrm{D}}$ 0,94–3,17, mostly 1,80–2,85 in *var. trichoceros*, mostly 1,15–1,80 in *var. contrarium;* $\frac{\mathrm{R90}}{\mathrm{D}}$ 1,78–5,95, mostly 2,50–4,00 in *var. trichoceros*, mostly 1,90–2,50 in *var. contrarium;* ratio $\frac{\mathrm{B}}{\mathrm{H}}$ difficult to calculate because of incomplete formation of girdle, varies from 0,40–2,80 in specimens measured, is usually higher in *var. trichoceros* than in *var. contrarium.*

Thecal ornamentation: Variation in girdle development has been discussed; thecal wall generally thin; smooth margined list usually present between base of hypotheca and left horn; minute spines sometimes present along lower edge of proximal parts of antapical horns in *var. trichoceros*, very rarely in *var. contrarium*, (Karsten (1906) Pl. 22, fig. 32b, shows spines along upper edges of antapical horns as well); minute spines may be present on either side of proximal part of apical horn. In *var. contrarium*, tips of antapical horns occasionally clavate to a varying degree, this inflation sometimes retuse; inflated tips apparently not recorded for *var. trichoceros;* apical horn sometimes inflated for almost entire length and ornamented with minute spines, mostly found in *var. trichoceros;* in specimens of *var. contrarium* with inflated antapical horn tips, tip of apical horn sometimes inflated. Some specimens of *var. contrarium* with markedly thickened thecal walls and incompletely formed girdles were seen in the Agulhas current NGY station 41 immediately off Port Elizabeth. (Refer to account of distribution of *C. tenue.*)

In the Agulhas current NGY samples, all specimens with a girdle diameter

NGY STATIONS	11*	12	13	14	15	16		41*	42	43	44	45	46	
Surface temperature	20,66	24,28	25,49	23,78	22,19	21,62		17,49	23,27	24,15	23,50	21,25	20,90	
Temperature at 100m	13,26 (at 50m)	17,53	19,65	19,52	18,73	18,61		16,66 (at 50m)	12,21	19,99	20,54	20,50	20,37	
Number slides examined	4	4	4	4	4	8		4	5	7	4	4	5	
Number ceratia counted	601	191	233	267	270	241	1803	318	92	197	184	241	365	1397
CERATIUM TRICHOCEROS	3,99%	19,37%	12,88%	11,24%	4,44%	3,32%	7,26%	1,57%	22,83%	8,12%	13,04%	8,71%	11,78%	9,31%
Random selection (Diam $\leq 42\,\mu$	9	18	9	4	4	5	49	-	5	1	6	-	3	15)
of measured (Diam = $45\,\mu$	-	-	1	1	1	-	3	-	-	-	-	-	-	-)
specimens (Diam $\geq 48\,\mu$	5	6	14	13	6	2	40	3	-	-	10	-	14	27)
CERATIUM MASSILIENSE VAR. MASSILIENSE	2,50%	5,24%	3,86%	0,75%	0,37%	1,66%	2,27%	2,52%	2,17%	3,55%	1,09%	1,66%	1,64%	2,08%
Random selection (A $\geq 90^\circ$	2	-	2	-	-	-	4	1	-	2	-	-	-	3)
of measured ($70^\circ \leq$ A $< 90^\circ$	8	6	4	-	1	1	20	5	1	3	1	3	2	15)
specimens ($50^\circ \leq$ A $< 70^\circ$	3	1	-	1	-	-	5	-	-	-	-	-	-	-)
CERATIUM MASSILIENSE VAR. CARRIENSE	-	2,09%	-	-	-	0,41%	0,28%	-	-	0,51%	2,72%	1,66%	-	0,72%
Random selection (B $> 130^\circ$	-	3	-	-	-	-	3	-	-	-	2	1	-	3)
of specimens (B $< 130^\circ$	-	1	-	-	-	1	2	-	-	1	3	3	-	7)
CERATIUM DEFLEXUM F. DEFLEXUM	-	1,57%	1,29%	1,87%	1,11%	0,41%	0,83%	0,69%	3,26%	0,51%	0,54%	0,41%	-	0,50%
CERATIUM DEFLEXUM F. DEFLECTOMASSUM	-	-	-	-	0,37%	-	0,06%	-	-	0,51%	0,54%	0,41%	0,55%	0,36%
CERATIUM MACROCEROS	-	-	5,58%	2,62%	1,48%	2,90%	1,72%	0,31%	1,09%	8,63%	5,98%	6,64%	3,84%	4,22%
CERATIUM TENUE	0,33%	7,85%	11,58%	6,36%	4,44%	4,14%	4,60%	6,28%	16,30%	7,61%	11,95%	12,03%	11,23%	10,16%

TABLE 1.

Showing distribution and relative frequency, expressed as a percentage, of species of Subsection *Macroceras* in samples from the line of NGY stations off Port Elizabeth, which were examined in detail for the *Ceratium* flora. (Temperatures in °C. A = Left horn degree co-ordinate with 15 μ radius co-ordinate, B = Left horn degree co-ordinate with 300 μ radius co-ordinate.) For hydrographic data from the Agulhas current NGY stations, see Zoutendyk (1960).

	No. NGY stns where ceratia recorded			Range of temps where ceratia recorded		Highest % abundance
	Feb-March (15 stns)	May (29 stns)	August (32 stns)	Highest s. temp (+ temp at 100m)	Lowest s. temp (+ temp at 100m)	in diatom-dinoflag. count per station
C. VULTUR F. SUMATRANUM	(1)*	1	-	26,04 19,07	25,11 21,30	0,31%
C. MACROCEROS	3(1)*	7	2	27,11 22,31	15,89 15,39(40m)	1,23%
C. DEFLEXUM F. DEFLEXUM	1(1)*	1	-	27,11 22,31	24,17 20,88	0,32%
C. DEFLEXUM F. DEFLECTOMASSUM	1	-	-	26,38 19,70	26,38 19,79	0,32%
C. MASSILIENSE V. MASSILIENSE	2(1)*	5	-	27,11 22,31	18,03 15,49	0,61%
C. MASSILIENSE V. CARRIENSE	1	2	-	25,49 19,65	24,17 20,88	0,31%
C. TENUE	3	9	8	27,11 22,31	15,89 15,39(40m)	1,25%
C. TRICHOCEROS	3(2)*	13	5(1)*	27,11 22,31	15,96 10,45	1,23%

TABLE 2.

Showing frequency of species of Section *Macroceras* Ostf. in the general diatom-dinoflagellate counts for Agulhas current NGY stations. (76 N50V net samples were taken over three cruises during I.G.Y. 1958. The relative frequency of phytoplanton taxa was assessed by examining diluted drops of samples and enumerating the first 300–600 diatom cells, plus any dinoflagellates encountered. A total of 30 313 diatom cells and 874 armored dinoflagellates, of which 417 were ceratia, was counted.) * = stations where taxa were observed, but not during the count.

≥ 45 μ could be classified as *var. contrarium*, and those with a diameter < 45 μ as *var. trichoceros*, because of the nature of the base of the left horn and overall antapical horn curvature. In the literature, when the diameter can only be calculated from the figure, it is sometimes difficult to decide which variety is being described, particularly when the scale is doubtful, as in the cases of Cleve's figure of "*C. flagelliferum*" and Schiller's figure of *C. trichoceros*, by implication of *var. trichoceros*, (1937, Fig. 470), where the diameters are estimated as ≤ 42 μ, but antapical horn curvature and the nature of the base of the left horn, especially in Schiller's figure, are more typical of *var. contrarium*. Steemann Nielsen (1934) treated specimens from the Dana Pacific stations with diameters < 42 μ as *C. trichoceros* and ≥ 45 μ as '*C. contrarium*'.

Apical horn length varies from about 150–600 μ; in NGY specimens, there was little difference in horn length between the varieties; tips of antapical horns were generally below level of apex of apical horn, sometimes tips of all three horns were at same level; Entz (1902 Fig. 43) depicts a specimen of *C. trichoceros*, variety uncertain, in which the length of the antapical horns exceeds that of the long apical horn.

Distribution: C. trichoceros is a common species recorded from all oceans and the Mediterranean. Steemann Nielsen (1934, 1939) considered both *var. trichoceros* and *var. contrarium* to be surface species, but Graham & Bronikowsky (1944) found more records of *var. trichoceros* at 100 m than at upper levels in the Carnegie samples. Both authors found *var. contrarium* in tropical and subtropical waters, while *var. trichoceros* appeared to be a more strictly tropical taxon. *In situ* temperatures recorded by Graham & Bronikowsky for *var. trichoceros* were 14,0–29,4°C, and for *var. contrarium*, 10,2–29,5°C. Steemann Nielsen and Sournia (1967) found *var. trichoceros* to be indifferently oceanic and neritic, and *var. contrarium* clearly oceanic. This is supported by the records of Davis & Steidinger (1966) and Steidinger & Williams (1970) for neritic waters off Florida. In the numerical survey of Agulhas current NGY stations phytoplankton, a distinction between the two varieties was, unfortunately, not made. However, random measurements of girdle diameters show that for the neritic stations off Port Elizabeth, NGY 11 and 41, at least 5/24 and 3/5 specimens, respectively, could be classified as *var. contrarium*. (See Tables 1 and 2.)

Earlier records for the Agulhas current and S. W. Indian ocean are those of Karsten (1907) and Nel (1968), who used Karsten's nomenclature, recording *C. trichoceros*, '*C. tripos flagelliferum*', and its varieties '*angusta*', '*crassa*' and '*major*', Taylor (1967) and Thorrington Smith (1969), both of whom did not distinguish between the varieties.

Ceratium trichoceros var. trichoceros

C. trichoceros (Ehrenberg) Kofoid (1908a): 362, Fig. 16–19; (1908b): 338;

Jörgensen (1911): 75, Pl. 9, Fig. 159a, b; (1920): 95, Fig. 85; Schröder (1911): 647 (as *C. trichoceras*); Forti (1922): 71, Pl. 5, Fig. 57 (= Jörgensen Fig. 159a); Pavillard (1931): 90, Pl. 3, Fig. 4; Böhm (1931a): 363; (1931b): 40; Wang & Nie (1932): 303, Fig. 15; Peters (1932): 51, Pl. 1, Fig. 3a–c, *non* Pl. 4, Fig. 17a (= *var. contrarium*); Steemann Nielsen (1934): 27, Fig. 68; (1939): 15; Nie (1936): 70, Fig. 32a, b and ? c (could be *var. contrarium*); Schiller (1937): 430, Fig. 470; Graham & Bronikowsky (1944): 40, Fig. 22B; Silva (1949): 361, Pl. 7, Fig. 4; Wood (1954): 311, Fig. 239a; Halim (1960): 180, Pl. 5, Fig. 18; (1963): 499, Fig. 31; Ballantine (1961): 225, Fig. 57; Klement (1964): 358; López (1966): 333, Figs. 44, 45; Davis & Steidinger (1966) Figs. 1–4; Sournia (1967): 472, Fig. 89; Steidinger & Williams (1970): 47, p.p., Fig. 36a–d, (includes *var. contrarium*).

C. flagelliferum Cleve (1900a): 14, e.p., Pl. 7, Fig. 12; (1900b): 217, e.p.; (both include *var. contrarium*); Okamura & Nishikawa (1904): 123, Pl. 1, Fig. 6 *non* 7 (= *var. contrarium*).

C. tripos flagelliferum (Cleve) Karsten (1906): 145, 148, Pl. 22, Fig. 31b *non* 31a, c, d (= *var. contrarium*).

C. tripos flagelliferum f. crassa Karsten (1906): 146, 148, Pl. 22, Fig. 32a *non* b (= *var. contrarium*); *nec* Karsten (1907) Pl. 49, Fig. 25a–c (= *C. massiliense var. massiliense*).

C. tripos flagelliferum f. atlantica Stüwe (1909): 274, Pl. 1, Fig. 10 (if scale correct).

C. trichoceros f. crassum (Karst.) Jörgensen (1911): 76.

C. contrarium: Margalef (1957): 47, Fig. 3f; Paredes (1969/70): 42, e.p., Pl. 21, Fig. 147 (includes *var. contrarium*).

C. trichoceros var. contrarium: Klement (1964): 358, Pl. 3, Fig. 5.

Peridinium trichoceros Ehrenberg (1860): 791; (1873): 3, Pl. 1, Fig. 1.

? *Non C. flagelliferum var. filiformis* Okamura & Nishikawa (1904): 123, Pl. 1, Fig. 11 (? = *C. tenue*).

Nomen nudum: C. tripos var. flagellifera Cleve (1899): 3.

Diagnosis: Differs from *var. contrarium* in having the girdle diameter $<$ 45 μ, or a diameter 45–48 μ and a "kink" at the base of the left horn and/or the ratio $\frac{\text{RMBC}}{\text{D}}$ exceeding 1,75.

Dimensions: In NGY specimens: Girdle diameter 30–42 μ, mostly 36–42 μ; length left profile of hypotheca from base of horn to lower girdle list, 18–27 μ; length epitheca, seen dorsally, from centre of upper girdle list to base of apical horn, 15–27 μ; length apical horn 150–465 μ. *From literature:* diameter: 37–48 μ (Jörgensen (1911), 31–42 μ (Böhm 1931b), 40 μ (Wang & Nie 1932): 33–42 μ (Steemann Nielsen 1932), 41–45 μ (Silva 1949), 40 μ (Halim 1960), 44 μ (Halim 1963), 43 μ (Klement 1964), 38,4–45,5 μ (Davis & Steindinger 1966), as low as 31

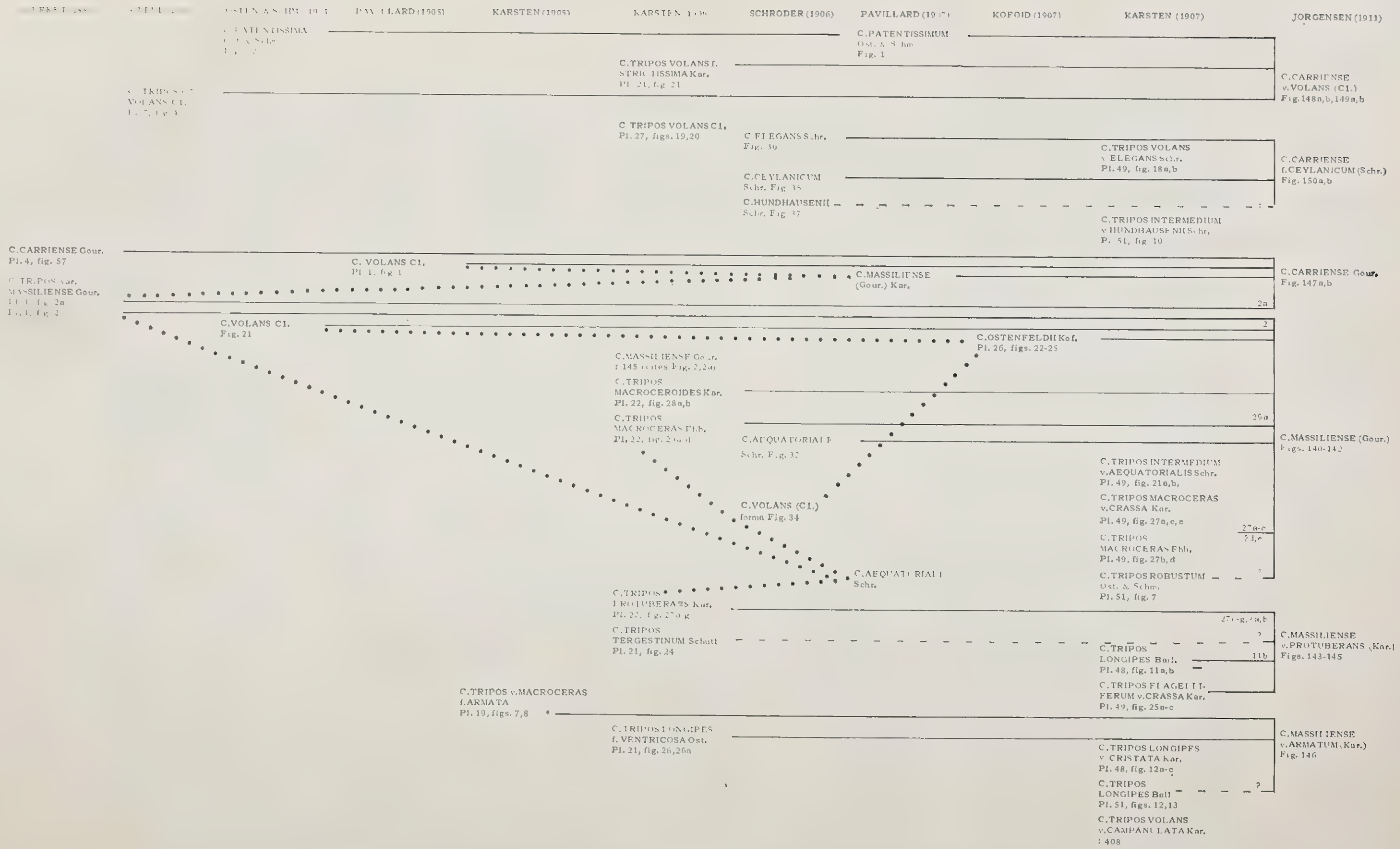

TABLE 3.
Chart showing taxonomic history of *C. massiliense* (Gour.) Karst. up to 1911, with Jörgensen's and other authors' interpretation of previously described taxa.

μ (Steidinger & Williams 1970, who included specimens of *var. contrarium* with diameters $> 48\ \mu$ in the range of measurements given); length apical horn 200–420 μ (Jörgensen 1911).

Böhm (l.c.), on examination of 208 specimens at 7 stations, found that diameter decreased with increase in temperature. This was confirmed by Steemann Nielsen (1934), who also found that the diameter tended to increase in size in neritic conditions; he found further, that antapical horns tended to be shorter in specimens from oceanic stations. These observations were not supported by random measurements of NGY Agulhas current specimens.

Ceratium trichoceros var. contrarium (Gourret) Schiller (1937): 431, Fig. 471 (= Jörgensen (1911) Fig. 160a).
Rampi (1939): 310, Fig. 39; Wood (1954): 311, Fig. 239b; Steidinger & Williams (1970): 47; *non* Klement (1964): 358, Pl. 3, Fig. 5 (= *var. trichoceros*).
C. tripos var. contrarium Gourret (1883): 32, Pl. 3, Fig. 51.
C. tripos contrarium: Karsten (1906): 145, 147, Pl. 22, Fig. 30a, b.
C. contrarium (Gourret) Pavillard (1905): 53, Pl. 2, Fig. 1; (1907): 229; (1931): 89, Pl. 3, Fig. 3; (1937): 9; Jörgensen (1920): 93, Fig. 84; Paulsen (1930): 90, Fig. 58A–C; Böhm (1931a): 363; (1931b): 40; Peters (1932): 50, Pl. 2, Fig. 10c; Steemann Nielsen (1934): 27, Fig. 67; (1939): 15; Graham & Bronikowsky (1944): 40, Fig. 24A *non* 22E (= *C. massiliense*); Silva (1949): 361, Pl. 9, Fig. 12; Halim (1960): 179; (1963): 499, Fig. 30; Margalef & Duran (1953): 42; Wood (1963): 7; López (1966): 333, Fig. 46; Sournia (1967): 472, Fig. 89; Paredes (1969/70): 42, e.p., *non* Pl. 21, Fig. 147 (= *var. trichoceros*); *non* Margalef (1957): 47 Fig. 3f (= *var. trichoceros*).
C. tripos var. macroceras f. contraria (Gourret) Schröder (1901): 16.
C. tripos var. inflexum Gourret (1883): 29, Pl. 3, Fig. 44.
C. inflexum (Gourret) Kofoid (1908b): 388; Jörgensen (1911): 76, Pl. 9, Figs. 160a, b, 161 a, b; Schröder (1911): 647; Pavillard (1916): 18; Forti (1922): 72, Pl. 5, Fig. 58 (= Jörgensen Fig. 161a); Abè (1927): 432, Fig. 50; *non* Schröder (1906): 362 (belongs to Section *Tripos*, as Schröder describes the "antapex" as "etwas gewolbt").
? *C. tripos var. macroceras f. inflexa* (Gourret) Schröder (1900): 16, e.p., *non* Pl. 1, Fig. 17h (= *C. contortum var. karstenii* (Pav.) Sour. according to Jörgensen (1920: 75)).
C. flagelliferum Cleve (1900a): 14, e.p., non Pl. 7, Fig. 12 (= *var. trichoceros*); (1900b): 217, p.p., (includes *var. trichoceros*).
C. tripos flagelliferum (Cleve) Karsten (1906): 145, 148, Pl. 22, Fig. 31 a, c, d. *non* b (= *var. trichoceros*).
C. tripos flagelliferum f. crassa Karsten (1906): 146, 148 Pl. 22, Fig. 32b *non* a (= *var. trichoceros*); *non* (1907): 410, Pl. 49, Fig. 25a–c (= *C. massiliense*).

LEFT HORN DEGREE COORDINATE WITH THE 150 μ RADIUS COORDINATE

<120°	120–124°	125–129°	130–134°	135–139°	≥140°
?GO 83 57 CC 63,70					
?GO 83 2A CTM 75		?GO 83 2A CTM 60			?GO 83 2 CTM 60,75
+CL 00 4 CV 64					
?OS 01 22 CP 67					
?OS 01 21 CV 75	?OS 01 21 CV 69				
?PA 07 1A CP 69			?PA 05 1 CV 69		
?PA 07 1B CP 70					
?PA 16 4 CCV 69					
?PA 23 C CCVP 63,69		+PA 31 6 CC 74			
*SH 06 35 CC 90					*SH 06 32 CA 100
*SH 06 36 CE 108					*SH 06 34 CV 88
*SH 06 37 CH 90					
*KA 06 19A CTV 104					
*KA 06 19B CTV 96					
*KA 06 21 CTVS 96					
*KA 07 18A CTVE 72					
*KA 07 18B CTVE 88					
*KA 07 27D CTM 88					
*KA 07 27E CTMC 104					
*OK 07 2A CP<65,>65					
*OK 07 2B CP<65,>65					
+OK 07 2C CP 70					+OK 07 18D CV 62
+OK 07 18B CV 72				+OK 07 18C CV 64	*OK 07 18E CV≥60
	+KO 07 25 CO 73				+KO 07 22 CO 73
+JO 11 148 CCV 63	+JO 11 147 CC 72	?JO 11 150 CC 60,66			+KO 07 23 CO 66
?JO 11 149 CCV 60,69					
+FO 22 54 CC 75					
+PU 30 57A CC 75					
+PU 30 57C CC 63					
?BO 31 18B CME 66	?BO 31 17B CME 66	?BO 31 18A CME 75			?BO 31 17A CME 60,69
+SN 34 64 CCV 64					
+SL 37 464B CC 60					
+GB 44 22A CC 75					
?MD 53 12L CCV 70			?MD 53 12N CM 73	?MD 53 12M CM 66	?MD 53 12K CH 73
+HA 60 11 CCV 72					
+HA 63 28 CMM 66					
+LO 66 47 CC 63					
+LO 66 48 CC 63	+LO 66 48 CC 65				
+LO 66 49 CCV 70	+LO 66 50 CM 70				
+LO 66 51 CM 80					
?SW 70 13A CC 66					
?SW 70 14A CCV 72					
-NGYNGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY				
NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY		NGYNGYNGYNGYNGYNGY	+ 49 SPECIMENS
NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY		NGYNGYNGYNGYNGYNGY	NGYNGYNGYNGYNGYNGY

LEFT HORN DEGREE COORDINATE WITH 300 µ RADIUS COORDINATE

< 120°	120-129°	130-139°	≥ 140°	≥ 140°
?GO 83 57 CC 63,70	?GO 83 57 CC 63,70	?GO 83 57 CC 70	?GO 83 2A CTM 60,75	?GO 83 2 CTM 60,75
+CL 00 4 CV 64	+CL 00 4 CV 64	+CL 00 4 CV 64		
?OS 01 22 CP 67		?OS 01 21 CV 69,75		
?PA 07 1A CP 69	?PA 16 4 CCV 69	+PA 31 6 CC 74		
?PA 07 1B CP 70				?PA 05 1 CV 69
?PA 23 C CCVP 63,69				
*SH 06 35 CC 90	*SH 06 37 CH 90			
*SH 06 36 CE 108				*SH 06 34 CV 88
*KA 06 19A CTV 104	*KA 06 19B CTV 96			*SH 06 32 CA 100
*KA 06 21 CTVS 96				
*KA 07 18A CTVE 72	*KA 07 27D CTM 88	*KA 07 27E CTMC 104		
*KA 07 18B CTVE 88				
+OK 07 2C CP 70	*OK 07 2A CP>65	*OK 07 2A CP<65		+OK 07 18C CV 64
*OK 07 2B CP>65	*OK 07 2B CP<65			+OK 07 18D CV 62
+OK 07 18B CV 72				*OK 07 18E CV≥60
			+KO 07 25 CO 73	+KO 07 22 CO 73
+JO 11 148 CCV 63		+JO 11 147 CC 72		+KO 07 23 CO 66
?JO 11 149 CCV 60,69		?JO 11 150 CCC 60,66		
		+FO 22 54 CC 75		
+PU 30 57A CC 75			+PU 30 57C CC 63	
	?BO 31 18B CME 66		?BO 31 18A CME 75	?BO 31 17A CME 60,69
			?BO 31 17B CME 66	
+GB 44 22A CC 75	+SN 34 64 CCV 64		+SL 37 464B CC 60	
		?MD 53 12L CCV 70		?MD 53 12K CH 73
			+HA 60 11 CCV 72	?MD 53 12M CM 66
			+HA 63 28 CMM 66	?MD 53 12N CM 73
	+LO 66 49 CCV 70	+LO 66 47 CC 63	+LO 66 48 CC 65	
		+LO 66 51 CM 80	+LO 66 50 CM 70	
?SW 70 14A CCV 72		?SW 70 13A CC 66		
NGYNGYNGYNGYNGYNGY				
NGYNGYNGYNGYNGYNGY	NGYNGYNGYNGYNGYNGY			
NGYNGYNGYNGYNGYNGY	NGYNGYNGYNGYNGYNGY		-NGYNGYNGYNGYNGYNGY	
NGYNGYNGYNGYNGYNGY	NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY	+ 49 SPECIMENS
NGYNGYNGYNGYNGYNGY	NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGYNGY	NGYNGYNGYNGYNGYNGY
LEFT HORN DEGREE COORDINATE WITH 150 µ RADIUS COORDINATE < 130°				LH°C AT 150 µ RC>130°
(VAR. CARRIENSE)				(VAR. MASSILIENSE)

TABLE 4.

Showing variation in left horn degree co-ordinates with the 150 and 300 μ radius co-ordinates in C *massiliense* (Gour.) Karst., in specimens from the Agulhas current NGY samples and in a selection of figures from the literature. The latter are referred to in sequence by author, year of publication, figure number, name used and diameter in μ which determined scale of photographic enlargement; in specimens underlined, co-ordinates are estimated. (BO Böhm, CL Cleve, FO Forti, GB Graham & Bronikowsky, GO Gourret, HA Halim, JO Jörgensen, KA Karsten, KO Kofoid, LO López, MD Margalef & Duran, OK Okamura, OS Ostenfeld & Schmidt, PA Pavillard, PU Paulsen, SH Schröder, SL Schiller, SN Steemann Nielsen, SW Steidinger & Williams; ? = original scale of figure not known, * = scale of figure known, but possibly incorrect, + = scale of figure known and probable, — = NGY specimens in which left horn degree co-ordinate with 300 μ radius co-ordinate is > 130°.)

	< 0,50	0,50 - 0,75	0,75 - 1,00	1,00 - 1,25	1,25 - 1,50	1,50 - 1,75	1,75 - 2,00	2,00 - 2,25	2,25 - 2,50	2,50 - 2,75	2,75 - 3,00	3,00 - 3,25	3,25 - 3,50	3,50 - 3,75	3,75 - 4,00
DIAM < 45 µ			STUW O&N6		MA3F SW36D CLEV XXXXX XXXXX	N32A WN15 SN68 SH470 XXXXX XXXXX	D&S3 D&S1 BA57 HA18 PE3B	HA31 PR147 SIL4 XXXXX XXXXX XXXXX XXXXX XXXXX XXXXX XXXXX	KLE5 J159A XXXXX XXXXX XXXXX XXXXX XXXXX XXXXX XXXXX	PAV4 XXXXX XXXXX	XXXXX XXXXX		GB22B	EHRB XXXXX	KOF16
DIAM 45-48 µ				SD17N* XXXXX XXXXX	GO51* XXXXX XXXXX XXXXX XXXXX XXXXX XXXXX	PE17A* XXXXX XXXXX XXXXX XXXXX	D&S3 D&S1	LO45	SO89 LO44 K32A PE3C	K31B		PE3A			
DIAM > 48 µ	K33A	SO90	PU58A RA39 RA38 XXXXX	J161A HA30 SIL7 LO46 PAV16 K22D AB50B AB50A GB24A GO36 XXXXX XXXXX XXXXX XXXXX XXXXX	HA14 O&N7 K30A J160A PU58C SN67 PAV3 GO44 XXXXX XXXXX XXXXX XXXXX XXXXX XXXXX	K22A GB24B XXXXX XXXXX	K32B K23 PE10C	K31A			AB49				

TABLE 5.

C. trichoceros (Ehb.) Kof.: Showing variation in the ratio $\frac{\text{RMBC}}{\text{D}}$ (right horn MBC radius co-ordinate in radius units/girdle diameter in radius units) in relation to the girdle diameter in specimens from NGY Agulhas current stations and from the literature. (AB, Abè (1927); BA, Ballantine (1961); CLEV, Cleve (1900a); D & S, Davis & Steidinger (1966); EHRB, Ehrenberg (1873); GB, Graham & Bronikowsky (1944); GO, Gourret (1883); HA, Halim (1960, 1963); J. Jörgensen (1911); K. Karsten (1906, 1907); KLE, Klement (1964); KOF, Kofoid (1908a); LO, López (1966); MA, Margalef (1957); N, Nie (1936); O&N, Okamura & Nishikawa (1904); PAV, Pavillard (1931); PR, Paredes (1969/70); PU, Paulsen (1930); RA Rampi (1939); SN, Steenmann Nielsen (1934); SW Steidinger & Williams (1970); SD, Schröder (1900); SH, Schiller (1937); SIL, Silva (1949); SO, Sournia (1967); STUW, Stuwe (1909); WN, Wang & Nie (1932); *indicates $\frac{\text{RMBC}}{\text{D}} < 1{,}75$ and basal "kink" absent in left horn; XXXXX refers to NGY specimens, where all with a girdle diameter $\geq 45\ \mu$, lacked a basal kink in the left

C. tripos flagelliferum f. angusta Karsten (1906): 146, 148, Pl. 22, Fig. 33a *non* b (= *C. tenue*).

C. tripos flagelliferum var. angusta Karsten (1907): 410, 411, Pl. 49, Fig. 24a, *non* b, c (b = *C. massiliense* (on account of size), c = *C. tenue*).

C. tripos flagelliferum var. major Karsten (1907): 410, Pl. 49, Fig. 22a–d.

C. tripos var. macroceras f. claviceps Schröder (1900): 16, Pl. 1, Fig. 17 n, (as Jörgensen (1920: 75) indicates, scales given by Schröder are incorrect).

C. inflexum f. claviceps (Schröder) Jörgensen (1911): 76; Schröder (1911): 647, Fig. 12.

C. trichoceros f. claviceps (Schröder) Schiller (1937): 431; Rampi (1939): 311; Wood (1954): 312, ? Fig 239c (in this figure, tips of antapical horns not shown), *non* Fig. 239d (unamed figure with clavate horn tips, from curvature of horns = *C. tenue*).

C. contrarium f. claviceps (Schröder) Jörgensen (1920): 94.

C. contrarium var. claviceps (Schröder) Graham & Bronikowsky (1944): 40, Fig. 24B; Halim (1960) Pl. 5, Fig. 14.

C. trichoceros var. contrarium f. claviceps: Davis & Steidinger (1966).

C. tripos flagelliferum var. undulata Karsten (1907): 410, Pl. 49, Fig. 23.

Non C. tripos macroceras f. undulata Schröder (1900): 16, Pl. 1, Fig. 17kum (k = *C. massiliense*, 1 = *c. tenue* (also according to Pavillard (1931) but not Jörgensen (1911, 1920) who considered it to be *var. contrarium*), m = *C. vultur var. pavillardii* (Jörg.) Rein. (considered by Jörgensen (1920: 87, 92 to be both *C. massiliense* and *var. pavillardii*).

C. tripos var. typicum Gourret (1883): 31, Pl. 2, Fig. 36; Daday (1888): 99.

C. tripos var. Gouretii Lemmermann (1901): 636.

C. trichoceros: Peters (1932): 51, e.p., Pl. 4, Fig. 17a (includes *var. trichoceros*); Abè (1927): 431, Fig. 49; Rampi (1939): 310, Fig. 39.

C. horridum subsp. tenue: Dangeard (1927): 379, Fig. 43a, *non C. tenue* O. & S.

C. massiliense: Paulsen (1930) Fig. 55A, B *non* C–F (= *C. massiliense*), *non C. massiliense* (Gourret) Karsten.

"Typenkreise der Gattung *Ceratium*": Schütt (1892): 267, Fig. 77Vb.

Diagnosis: Differs from *var. trichoceros* in that the girdle diameter is $> 48\ \mu$, or 45–48 μ with the ratio $\frac{\text{RMBC}}{\text{D}} < 1{,}75$ and no "kink" at base of left horn·

Dimensions: In NGY specimens: Girdle diameter 45–60 μ, mostly 48–54 μ; length hypotheca 24–39 μ; length epitheca 21–36 μ; length apical horn 160–620 μ. *From literature:* diameter: 51–68 μ (Jörgensen 1911), 59–64 μ (Paulsen 1930), 45–60 μ (Steemann Nielsen 1934), 48 μ (Paredes 1969/70), up to 61 μ (Steidinger & Williams 1970, who included specimens of *var. trichoceros*, with diameters $< 45\ \mu$ in the range of measurements given); apical horn 300–560 μ (Jörgensen 1911).

Steemann Nielsen (1934) found that diameter showed an increase in size with a decrease in temperature. Random measurements of NGY specimens were insufficient to substantiate this.

The distal parts of the apical and antapical horns generally lie parallel to one another: six specimens were found in the NGY samples where the antapical horns diverged to a varying degree from one another and the apical horn. These were similar to cells referred to by Karsten (1907) as *C. tripos flagelliferum var. major.* In the graphs of antapical horn curvature they are shown separately as *var. contrarium* B, but they do not differ sufficiently to be treated as a distinct taxon, (See Figs. 13A–C, 24E).

The separation of specimens with clavate antapical horn tips as a distinct taxon is not justified, as a range of variation, from antapical horns with rounded, to slightly clavate, to very expanded tips, is found. Graham & Bronikowsky (1944) found specimens with clavate tips rather frequent in the N. Atlantic and Pacific; they were not recorded by Sournia (1967) and only two were seen in the present survey.

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References

Abé, T. H., 1927. Report of the biological survey of Mutsu Bay. 3. Notes on the protozoan fauna of Mutsu Bay. *1.* Peridiniales: *Ceratium* Schrank. *Sci. Rep. Tôhoku Univ.* Ser. 4, **2** (4): 423–432.

Ballantine, D., 1961. *Gymnodinium chukwanii* n. sp. and other marine dinoflagellates collected in the vicinity of Zanzibar. *J. Protozool.* **8** (2): 217–228.

Bergh, R. S., 1882. Der Organismus der Cilioflagellaten. Eine phylogenetische Studie. *Morph. Jb.* **7:** 117–288, Pls 12–16.

Böhm, A., 1931a. Die Adriatischen Ceratien. *Bot. Arch.* **31** (3–4): 349–385.

———, 1931b. Distribution and variability of *Ceratium* in the Northern and Western Pacific. *Bull. Bernice P. Bishop Mus.* **87:** 3–46, Pl. 1.

Braarud, T., Fφyn, B. and Hasle, G. R., 1958. The marine and fresh-water phytoplankton of the Dramsfjord and the adjacent part of the Oslofjord March–December 1951. *Hvalråd. Skr.* **43.**

Cassie, V., 1961. Marine phytoplankton in New Zealand waters. *Botanica mar.* **2** Suppl.: 7–54, Pls 1–8.

Chun, C., 1903. Uit de Diepten der Wereldzee. *Schilderungen von der Deutschen Tiefsee-Expedition.* Nederlands Edition. W. J. Thieme & Cie, Zutphen.

Claparéde, E. and Lachmann, J., 1859. Études sur les Infusoires et les Rhizopodes. *Mém. Inst. natn. génev.* **6** (1): 261–282, Pls 14–24.

Cleve, P. T., 1897. Report on the phytoplankton collected on the expedition of H.M.S. 'Research' 1896. *A. Rep. Fishery Bd Scotl.* **15** (3): 297–304, Pl. 1.

———, 1899. Plankton collected by the Swedish expedition to Spitzberg in 1898. *K. svenska VetenskAkad. Handl.* **32** (3): 1–51, Pls. 1–4.

———, 1900a. Notes on some Atlantic plankton-organisms. *Ibid.* **34** (1): 3–22, Pls. 1–8.

———, 1900b. The seasonal distribution of Atlantic plankton-organisms. *Göteborgs K. Vetensk.-o. VitterhSamh. Handl.* Ser. 4, **3:** 1–368.

Daday, E., 1888. Systematische Übersicht der Dinoflagellaten des Golfes von Neapel. *Természettud. Füz.* **11** (2): 98–104, Pl. 3.

Dangeard, P., 1926. Description des Péridiniens testacés recueillis par la mission Charcot pendant le mois d'août 1924. *Annls Inst. océanogr., Monaco* Nouv. Ser. **3:** 307–334.

———, 1927. Phytoplancton de la croisère du Sylvana. *Ibid.* **4** (8): 286–405.

Davis J. T. and Steidinger, K. A., 1966. *Ceratium trichoceros* (Ehrenberg) Kofoid. *Fla Bd Conserv. mar. Lab. Leafl. Ser.* **1.**

Ehrenberg, C. G., 1840. Beobachtungen von 274 Infusorienarten. *Ber. Verh. K. preuss. Akad. Wiss. Berl.*: 201.

———, 1860. Über das Leuchten und über neue mikroskopische Leuchthiere des Mittelmeeres. *Mber. dt. Akad. Wiss. Berl.*: 791.

———, 1873. Die das Funkeln und Aufblitzen des Mittelmeeres bewirkenden unsichtbar kleinen Lebensformen. *Sber. Ges. naturf. Freunde Berl., Festschrift:* 1–4, Pl. 1.

Entz, G., 1902. (Hungarian ed.)/1905 (German ed.). Beiträge zur Kenntnis der Peridineen. *Math. naturw. Ber. Ung.* **20:** 96–144.

Forti, A., 1922. *Ceratium* Schr. In: Ricerche su la flora pelagica (fitoplancton) di Quarto dei Mille (Mare Ligure). *Memorie R. Com. talassogr. ital.* **97:** 31–76, Pls. 1–5.

Gaarder, K. R., 1954. Dinoflagellatae from the 'Michael Sars' North Atlantic deep-sea Expedition 1910. *Rep. scient. Results Michael Sars N.Atlant. deep Sea Exped.* **2** (3): 1–62.

Gourret, P., 1883. Sur les Péridiniens du golfe de Marseille. *Annls Mus. Hist. nat. Marseille,* **1:** 1–114, Pls. 1–4.

Graham, H. W., 1941. An oceanographic consideration of the dinoflagellate genus *Ceratium. Ecol. Monogr.* **11** (1): 101–116.

Graham, H. W. and Bronikowsky, N., 1944. The genus *Ceratium* in the Pacific and North Atlantic oceans. *Publs Carnegie Instn* **565**

Gran, H. H., 1902. *Ceratium* Schr. In: Das Plankton des Norwegischen Nordmeeres. *Rep. Norw. Fishery mar. Invest.* **2** (2) no. 5: 192–197.

Halim, Y., 1960. Étude quantitative et qualitative du cycle des Dinoflagellés dans les eaux de Villefranche-Sur-Mer (1953–55). *Annls. Inst. océanogr., Monaco* **38** (2): 123–232, Pls. 1–5.

———, 1963. Microplancton des eaux égyptiennes. Le genre *Ceratium* Schrank (Dinoflagellés). *Rapp. P.-v. Réun. Commn int. Explor. scient. Mer Méditerr.* **17** (2): 495–502.

Hasle, G. R., 1969. An analysis of the phytoplankton of the Pacific Southern Ocean: abundance, composition and distribution during the 'Brategg' expedition, 1947–1948. *Hvalråd. Skr.* **42.**

Hensen, V., 1887. Über die Bestimmung des Plankton's oder des im Meeren treibenden Materials an Pflanzen und Thieren. *Ber. Komiss. wiss. Untersuch. dt. Meere, Kiel* **5** (12–16): 1–108, Pls. 1–6.

Jörgensen, E. 1899. Protophyten und Protozöen im Plankton aus der norwegischen Westküste. *Bergens Mus Årb. 1899* **6:** 3–112, Pls. 1–5.

———, 1905. Protist plankton of Northern Norwegian fiords (winter and spring 1899, 1900). *Bergens Mus. Skr.*: 111–113.

———, 1911. Die Ceratien. Eine kurze Monographie der Gattung *Ceratium* Schrank. *Int. Revue ges. Hydrobiol. Hydrogr.* **4** Biol. Spl. (1): 1–124, Pls. 1–10.

———, 1920. Mediterranean Ceratia. *Rep. Dan. oceanogr. Exped. Mediterr.* 1908–1910 **2** (Biol. J–K): 1–110.

Karsten, G., 1905. Das Phytoplankton des Antarktischen Meeres nach dem Material der deutschen Tiefsee-Expedition 1898–1899. *Wiss. Ergebn. dt. Tiefsee-Exped. "Valdivia"* **2** (2) no. 1.

———, 1906. Das Phytoplankton des Atlantischen Ozeans nach dem Material der deutschen Tiefsee-Expedition 1898–1899. *Ibid.* **2** (2) no. 2.

———, 1907. Das Indische Phytoplankton. *Ibid.* **2** (2) no. 3.

Klement, K. W., 1964. Armored dinoflagellates of the Gulf of California. *Bull. Scripps Instn Oceanogr.* **8** (5): 347–372, Pls. 1–3.

Kofoid, C. A., 1907a. New species of dinoflagellates. Reps. scient. results "Albatross" Exped. 9. *Bull. Mus. comp. Zool. Harv.* **50** (6): 163–207, Pls. 1–17.

———, 1907b. Dinoflagellata of the San Diego region, 3. Descriptions of new species. *Univ. Calif. Publs Zool.* **3** (13): 299–340, Pls. 22–33.

———, 1908a. Exuviation, autotomy and regeneration in *Ceratium. Ibid.* **4** (6): 346–386.

———, 1908b. Notes on some obscure species of *Ceratium. Ibid.* **4** (7): 387–393.

Lanjouw, J. *et al.*, 1966. *International Code of Botanical Nomenclature.* Utrecht.

Lebour, M. V., 1925. The dinoflagellates of Northern seas. *Mar. biol. Ass. U.K.* 1–250, Pls. 1–35.

Lemmermann, E., 1900. *Ceratium* Schr. in Ergebnisse einer Reise nach dem Pacific: Planktonalgen. *Abh. naturw. Ver. Bremen* **16** (2): 345–367, Pls. 1, 2.

López, J., 1966. Variación y regulación de la forma en el género *Ceratium. Investigación pesq.* **30:** 325–427.

Mangin, M. L., 1912. Phytoplancton de la croisère du René dans l'Atlantique (Sept. 1908). *Annls Inst. océanogr., Monaco* **4** (1): 1–66, Pls. 1, 2.

Margalef, R. and Durán, M., 1953. Microplancton de Vigo, de octubre de 1951 a septiembre de 1952. *Publnes Inst. Biol. apl., Barcelona* **23:** 5–78.

Margalef, R. 1957. Fitoplancton de las costas de Puerto Rico. *Investigación pesq.* **7:** 39–52.

Mulford, R. A., 1963. Distribution of the dinoflagellate genus *Ceratium* in the tidal and offshore waters of Virginia. *Chesapeake Sci.* **4** (2): 84–89.

Nel, E. A., 1968. The microplankton of the south-west Indian ocean. *Investl Rep. Div. Sea Fish. S. Afr.* **62.**

Nie, D., 1936. Dinoflagellates of the Hainan region 1. *Ceratium. Contr. biol. Lab. Sci. Soc. China Zool. Ser.* **12** (3): 29–73.

Okamura, K. and Nishikawa, T., 1904. A list of the species of *Ceratium* in Japan. *Annotnes zool. jap.* **5** (3): 121–131, Pl. 6.

Okamura, K., 1907. An annotated list of plankton microorganisms of the Japanese coast. *Ibid.* **6** (1): 125–151, Pls. 3–6.

Ostenfeld, C. G. and Schmidt, J, 1901. Plankton from the Red Sea and the Gulf of Aden. *Vidensk. Meddr dansk naturh Foren.* **25:** 141–182.

Ostenfeld, C. H., 1903. Phytoplankton from the sea around the Faeröes. In: E. Warming (ed.), *Botany of the Faeröes* **2:** 558–612. London: Weldon,

———, 1931. Concluding remarks on the plankton collected on the quarterly cruises in the years 1902–1908. *Bull. trimest. Résult. Crois. périod. Cons. perm. int. Explor. Mer* **4:** 599–672.

Paredes, J. F., 1969/70. Subsídios para o conhecimento do Plancton marinho de Cabo Verde. I–Diatomáceas, Silicoflagelados e Dinoflagelados. *Mems Inst. Invest. cient. Moçamb.* **10** Serie A: 3–143.

Paulsen, O., 1907. The Peridiniales of the Danish waters. *Meddr Kommn Havunders.* Plankton **1** (5): 1–26.

———, 1908. Peridiniales. In: Brandt & Apstein, (ed.), Nordisches Plankton *Bot. Teil* **18:** 1–124.

———, 1930. Études sur le microplancton de la mer d'Alboran. *Trab. Inst. esp. Oceanogr* **4:** 1–108.

Pavillard, J., 1905. Recherches sur la flore pélagique (phytoplancton) de l'etang de Thau. *Trav. Inst. Bot. Univ. Montpellier* Sér. mixte **2:** 1–113, Pls. 1–3.

———, 1907. Sur les *Ceratium* du Golfe du Lion 1 et 2. *Bull. Soc. bot. Fr.* **54:** 148–154, 225–231.

———, 1916. *Ceratium* Schr. in Recherches sur les Péridiniens du Golfe du Lion. *Trav. Inst. bot. Univ. Montpellier* Sér. mixte **4:** 9–70.

———, 1923. A propos de la systématique des Péridiniens. 1 et 2. *Bull. Soc. bot. Fr.* **70:** 876–882, 914–918.

———, 1931. Phytoplancton (Diatomées, Péridiniens) provenant des Campagnes scientifiques de S.A.S. le Prince Albert Ier de Monaco. *Résult. Camp. scient. Prince Albert I* **82:** 1–203, Pls 1–3.

———, 1937. Les Péridiniens et Diatomées pélagiques de la mer de Monaco de 1907 à 1914. Observations générales et conclusions. *Bull. Inst. océanogr. Monaco* **738:** 1–56.

PETERS, N., 1932. Die Bevolkerung des Südatlantischen Ozeans mit Ceratien. *Wiss. Ergebn. dt. atlant. Exped.* "*Meteor*" **12** (1): 1–69, Pls. 1–4.

RAMPI, L., 1939. Richerche sul Phytoplancton del Mare Ligure 1. I *Ceratium* delle acque di Sanremo. *Nuovo G. bot. ital.* **46:** 299–312.

———, 1942. Richerche sul Phytoplancton del Mare Ligure 4. I *Ceratium* delle acque di Sanremo Parte 2. *Ibid.* **49:** 221–236.

REINECKE, P., 1971. Studies in the genus *Ceratium* Schrank, with reference to specimens collected in the Agulhas current, in particular from a line of stations off Port Elizabeth during IGY 1958: 1. *Jl S. Afr. Bot.* **37** (2): 75–102.

———, 1973. Studies in the genus *Ceratium* Schrank with reference to specimens collected in the Agulhas current: 2. *Jl S. Afr. Bot.* **39** (1): 49–84.

SCHILLER, J., 1937. *Ceratium* Schr. in Dinoflagellatae (Peridineae). *Rabenhorst's Kryptogamen-Flora* **10** (3) 2: 349–432.

SCHRÖDER, B., 1900. Das Phytoplankton des Golfes von Neapel. *Mitt. zool. Stn Neapel* **14** (1–2): 1–38, Pl. 1.

———, 1906. Beiträge zur Kenntnis des Phytoplanktons warmer Meere. *Vjschr. naturf. Ges. Zürich* **51:** 319–377.

———, 1911. Adriatisches Phytoplankton. *Sber. Akad. Wiss. Wien, Abt.* 1 **120** (1): 601–687.

SCHUTT, F., 1892. Das Pflanzenleben der Hochsee. *Ergebn. Plankton-Exped. Humboldt-Stiftung* **1** A: 243–314.

SHIPLEY, A. M. and ZOUTENDYK, P., 1964. Hydrographic and Plankton data collected in the South West Indian Ocean during the SCOR International Indian Ocean Expedition 1962–1963. *Cape Town Univ. oceanogr. Dept. D.R.* **2.**

SILVA, E. S., and PINTO, J. S., 1948. O plancton da Baía de S. Martinho do Porto. *Bolm Soc. port. Ciênc.* **16** (2): 134–187, Pls. 1–6.

SILVA, E. S., 1949. Diatomáceas e dinoflagelados da Baía de Cascais. *Port. Acta biol.*, ser. B, vol. Julio Henriques: 300–383, Pls. 1–9.

———, 1955. Dinoflagelados do plâncton marinho de Angola. *Anais Jta Invest. Ultramar* **10** (2): 109–191, Pls. 1–11.

———, 1956. Contribuição para o estudo do microplâncton marinho de Moçambique. *Estudos Ensaios Docum. Jta Invest. Ultramar* **28:** 1–97, Pls. 1–14.

SOURNIA, A., 1966. Sur la variabilité infraspécifique du genre "*Ceratium*" (Péridinien planctonique) en milieu marin. *C. r. hebd. Séanc. Acad. Sci. Paris* **263:** 1980–1983.

———, 1967. Le genre *Ceratium* (Péridinien planctonique) dans le canal de Mozambique. Contribution a une révision mondiale. *Vie Milieu* Ser. A Biol. mar. **18** (2–3): 375–500.

STEEMANN NIELSEN, E., 1934. Untersuchungen über die Verbreitung, Biologie und Variation der Ceratien in Südlichen Stillen Ozean. *Dana Rep.* **1** (4): 3–67.

———, 1939. Die Ceratien des Indischen Ozeans und der Ostasiatischen Gewasser mit einer algemein Zuzammenfassung über die Verbreitung der Ceratien in den Weltmeeren. *Ibid.* no. 17.: 1–33.

STEIDINGER, K. A. and WILLIAMS, J., 1970. Dinoflagellates. *Fla. Dept. nat. Resour. mar. Res. Lab. Mem.* "*Hourglass*" *Cruises* **2:** 1–251, Pls. 1–45.

STEIN, F. R., 1883. Die Naturgeschichte der Arthrodelen Flagellaten. *Der Organismus der Infusionsthiere nach eigenen Forschungen in Systematischer Reihenfolge bearbeitet* **3** (2).

STÜWE, W., 1909. Phytoplankton aus dem Nord-Atlantik im Jahre 1898–1899. *Bot. Jb.* **43:** 225–302, Pls. 1, 2

TAYLOR, F. J. R., 1967. Phytoplankton of the South West Indian ocean. *Nova Hedwigia* **12** (3–4): 433–476, Pls. 88–96.

THORRINGTON-SMITH, M., 1969. Phytoplankton studies in the Agulhas current region off the Natal coast. *S. Afr. Ass. mar. biol. res. Inst. investl Rep.* **23.**

———, 1971. West Indian Ocean phytoplankton: a numerical investigation of phytohydrographic regions and their characteristic phytoplankton. *Mar. Biol.* **9** (2): 115–137.

TRAVERS, A. and M., 1962. Recherches sur le phytoplancton du golfe de Marseille. *Recl Trav. Stn mar. Endoume* **26** (41): 7–139.

VANHÖFFEN, E., 1897. Die Fauna und Flora Grönlands. *Grönland-Exped. Ges. Erdk. Berlin* 1891–1893 **2.**

VON STOTSCH, H. A., 1964. Zum Problem der sexuellen Fortpflanzung in der Peridineen-Gattung *Ceratium. Helgoländer wiss. Meeresunters.* **10** (1–4): 140–152.

WAILES, G. H., 1928. Dinoflagellates from British Columbia. Parts 1 and 2. *Mus. Art Notes, Vancouver* **3.**

WANG, C. C. and NIE, D. 1932. The genus *Ceratium* in a survey of the marine Protozoa of Amoy. *Contr. biol. Lab. Sci. Soc. China* (*Bot. Ser.*) **8** (9): 297–309.

WANG, C. C., 1936. The genus *Ceratium* in Dinoflagellates of the Gulf of Pê-Hai. *Sinensia, Nanking* **7** (2): 152–166.

WOOD, E. J. F., 1954. Dinoflagellates in the Australian region. *Aust. J. mar. Freshwat. Res.* **5** (2).

———, 1963. Checklist of Dinoflagellates recorded from the Indian Ocean. *Rep. Div. Fish. Oceanogr. C.S.I.R.O. Aust.* **28.**

ZACHARIAS, O., 1906. Über Periodizität, Variation und Verbreitung verscheidener Planktonwesen in südlichen Meeren. *Arch. Hydrobiol. Planktonk.* **1:** 498–575.

ZOUTENDYK, P., 1960. Hydrographic and plankton data collected in the Agulhas current during I.G.Y. *Cape Town Univ. oceanogr. Dept. Publ.* **1.**